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Cover photo: Marked female harvestman *Chavesincola inexpectabilis* with egg from southeastern Brazil. Photo by G. Machado.

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Reproductive behavior of *Chavesincola inexpectabilis* (Opiliones, Gonyleptidae) with description of a new and independently evolved case of paternal care in harvestmen

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Abstract. In this paper, we investigate the reproductive behavior of the gonyleptid *Chavesincola inexpectabilis* Soares & Soares 1946 (Heteropachylinae) and provide basic descriptive information about courtship, copulation, oviposition, and paternal care. Like most gonyleptids, males of *C. inexpectabilis* have a strong armature on the fourth pair of legs and use their spines and apophyses to fight other males and to repel them from their nesting sites. The mating pair interacts briefly before copulation, but the male touches the female both during and after penetration while she oviposits. The oviposition behavior differs markedly from that of other Laniatores: females hold the eggs on the chelicerae before depositing them on the substrate. After oviposition, the eggs are left under the guard of the male to defend against attack from cannibalistic conspecifics. Mapping the available data on reproductive biology of the Gonyleptidae on the phylogeny of the family, it is possible to infer that paternal care has evolved at least three times independently: once in the clade Progonyleptoidellinae + Caelopyginae, once in the Gonyleptinae, and once in the Heteropachylinae, which occupies a basal position within the group.

Keywords: Copulation, courtship, evolution, Heteropachylinae, oviposition, sexual dimorphism

The great majority of the harvestmen species reproduce sexually, although some species reproduce asexually by parthenogenesis (e.g., Phillipson 1959; Tsurusaki 1986). Fertilization is internal and the transfer of sperm may occur indirectly through spermatophores in representatives of the suborder Cyphophthalmi, or directly by means of a long and fully intromittent male genitalia in the suborders Eupnoi, Dyspnoi, and Laniatores (Machado & Macías-Ordóñez 2007). Courtship before intromission is generally quick and tactile, but there are some cases in which males offer a glandular secretion produced in their chelicerae before copulation as a nuptial gift for their mates. Courtship during intromission, on the other hand, may be longer and involve leg tapping and rubbing. Copulation is often followed by a period of mate guarding in which the female is held or constantly touched by the male (see table 12.1 in Machado & Macías-Ordóñez 2007).

Females may lay their eggs immediately or in the months after copulation, and the oviposition strategies seem to be related to the length of the ovipositor. Most species of the suborders Cyphophthalmi and Eupnoi have a long ovipositor and hide their eggs inside small holes in the soil, trunk crevices, or under stones. Representatives of the suborders Dyspnoi and Laniatores, constrained by their short ovipositor, lay their eggs on exposed substrates such as leaves, wood, and rocks (Machado & Macías-Ordóñez 2007). The forms of parental care range from microhabitat selection for oviposition to active egg guarding by a parental individual. In most species, eggs are laid singly in shallow natural cavities or are covered by debris by the female. In some species, however, females lay eggs in a single large clutch and brood eggs throughout the embryonic development, remaining with the newly hatched nymphs for some days until they disperse (Machado & Raimundo 2001). Maternal care has been reported for many families of the suborder Laniatores, especially among the

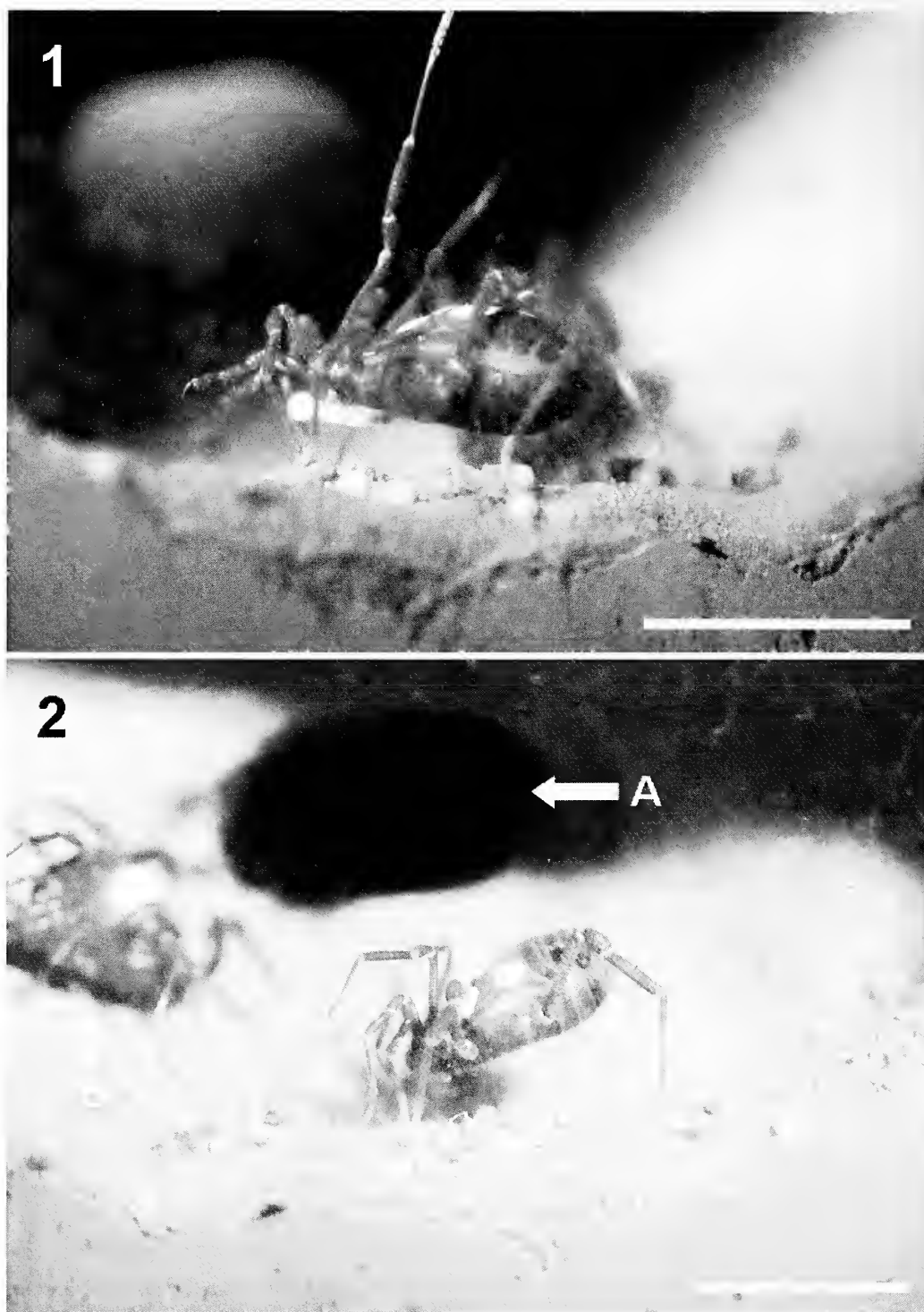
Neotropical representatives of the superfamily Gonyleptoidea (see Machado & Warfel 2006).

While maternal egg guarding is widespread among arachnids, exclusive paternal care is present only in the order Opiliones (Machado et al. 2004). Male assistance has evolved in at least five families belonging to three non-closely related superfamilies of the suborder Laniatores: Travunioidea, Epedanoidea, and Gonyleptoidea (Machado 2007). Within Gonyleptidae, which comprises nearly 1,000 species and corresponds to the largest family of Laniatores, there are eight cases of paternal care recorded so far (Machado & Macías-Ordóñez 2007). In this paper, we investigate the reproductive behavior of the gonyleptid *Chavesincola inexpectabilis* Soares & Soares 1946 (Heteropachylinae) and provide basic descriptive information about courtship, copulation, oviposition, and paternal care of this species. This study is the first description of the reproductive biology of a representative of the subfamily Heteropachylinae and the results obtained here represent a new and independently evolved case of paternal care in gonyleptid harvestmen.

METHODS

In all, 9 females and 14 males of *C. inexpectabilis* were collected along the borders of a small (ca 8 ha) urban forest fragment in Santa Teresa city (19°58'S; 40°32'W; elev. 675 m), Espírito Santo state, southeastern Brazil. The individuals were found under rotting logs and piles of tree fern trunks discarded from a green house nearby. They were brought to our laboratory in the Natural History Museum at Universidade Estadual de Campinas (São Paulo state, Brazil) and were maintained in a communal terrarium (40 × 90 cm base, 20 cm height) containing soil, small pieces of tree fern trunks collected in the study site, and 10 artificial nests built in clay blocks (with 6 × 2 cm base, 3 cm height). Each mud nest had a central hole (1 cm in diameter and 2 cm depth) crossing the clay block from side to side. These blocks were placed against

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Figures 1, 2.—1. Marked female of the harvestman *Chavesincola inexpectabilis* everting the ovipositor and manipulating the egg with the chelicerae while scrapping the substrate of the nest with her first pair of legs. 2. Another marked female covering a recently laid egg with debris. Behind the female, it is possible to see the nest entrance (A) and the guarding male walking around while she is ovipositing (B). Both photos were taken through the glass wall of the terrarium. Scale bars = 5 mm.

the glass wall of the terrarium so that it was possible to observe the harvestman behavior inside the nests through the glass (Figs. 1, 2). These mud nests simulated natural cavities in roadside banks, which are occupied by males of another Heteropachylinae species from Espírito Santo (*Pseudopucroliia* sp.). Males of *Pseudopucroliia* take care of the eggs laid by females inside these natural cavities, and the possession of

nests is crucial for their reproductive success (Nazareth & Machado unpubl. data). During the study period, the abiotic conditions in the laboratory were (mean \pm SD): temperature of $25.5 \pm 1.2^\circ\text{C}$, humidity of $82.0 \pm 5.4\%$, and photoperiod of 13L:11D.

Individuals were measured (dorsal scute width) and individually marked on their dorsal scute with colored dots

of enamel paint. They were fed pieces of dead cockroaches and an artificial diet for ants (Bhatkar & Whitcomb 1970) three times a week. The mud nests were individually numbered and, at each observation, the identity of the individuals inside each nest was recorded. Behavioral data are based on nearly 50 h of ad libitum observations (sensu Altman 1974), of which 43 h were conducted at night (from 18:00 to 00:00 h) when individuals were more active. Nocturnal observations were made with a red lamp to avoid disturbing the animals (cf. Elpino-Campos et al. 2001; Pereira et al. 2004). Continuous recording (sensu Martin & Bateson 1993) was made of all relevant behavioral events such as fights between males, copulations, and ovipositions. Voucher specimens of males and females were deposited in the arachnological collection of the Museu de Zoologia da Universidade de São Paulo (MZSP), São Paulo state, Brazil.

RESULTS

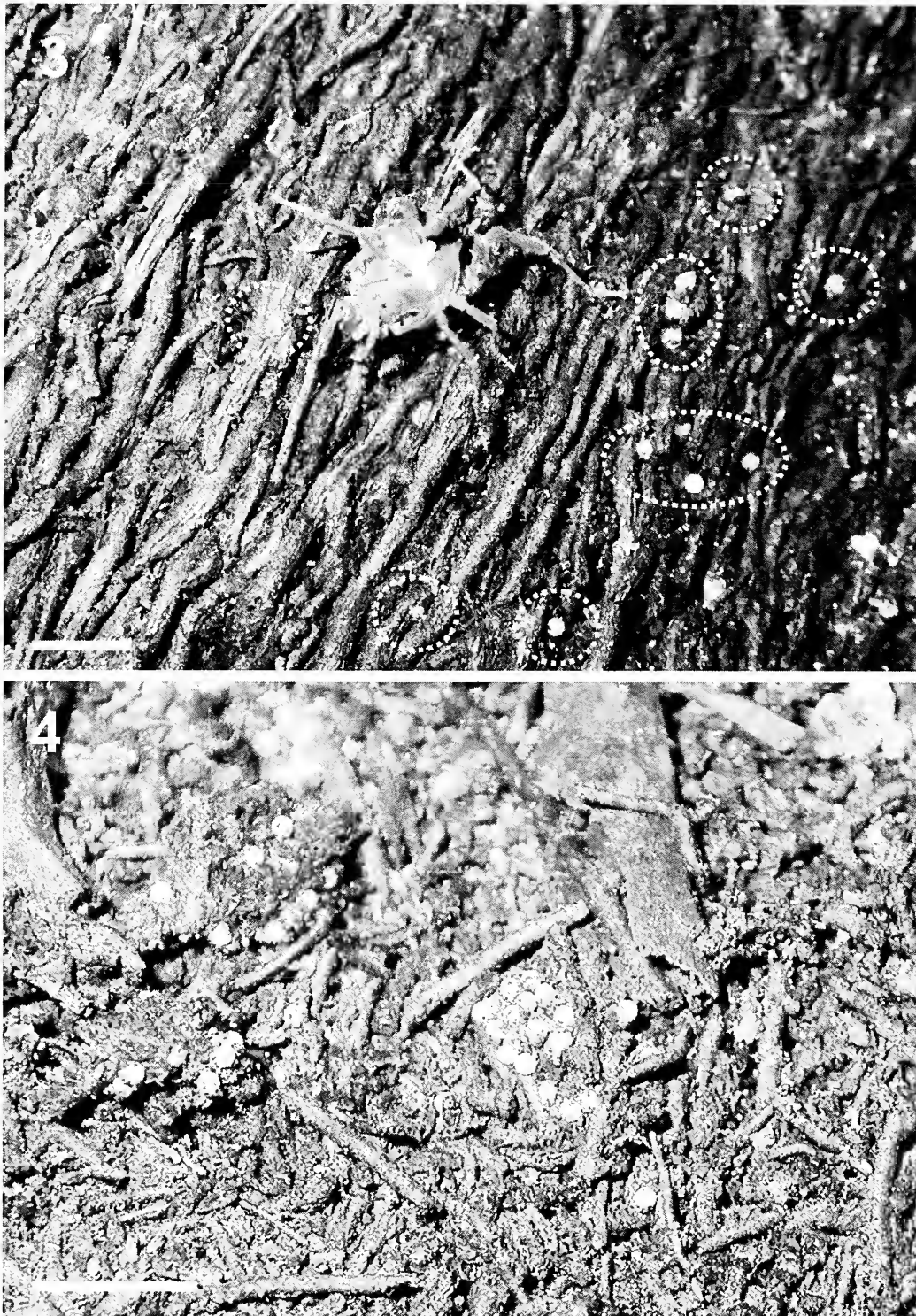
Nesting.—Ten males were observed occupying and occasionally fighting for the ownership of the mud nests. No fight or any kind of aggressive interaction was observed between males outside the nests. Only two males were observed mating: the first one (M1) achieved copulation after staying in the same mud nest for four consecutive days, and the second (M2), after five consecutive days. These males had a dorsal scute width of 4.99 mm (M1) and 4.71 mm (M2), and were, respectively, the first and the third largest males in the terrarium (mean male size \pm SD = 4.48 ± 0.27 mm; $n = 14$). On two occasions, as soon as an intruder male entered a mud nest occupied by one of these two males, a brief period of intense mutual tapping with the second pair of legs occurred. After that, the individuals turned their backs to each other and intertwined the fourth pair of legs, which bears many spines and tubercles. In this position, the males seemingly attempted to capsize each other by means of sudden upward movements in which each male brought its femur IV close to the body, pinching his opponent's fourth pair of legs, a behavior known as "nipping 2" (sensu Willemart et al. 2009). This phase of nipping 2 lasted nearly 30 s in the two fights observed and, in both cases, resident males managed to pull the intruders out of the mud nests.

Copulation.—All copulations occurred inside nests, and no sexual interaction between males and females were observed in other places of the terrarium. Most of the females (6 out of 9) were observed copulating at least once. One of them was observed copulating and laying eggs with M1 and M2 and another one was observed laying eggs twice with M1. M1 copulated at least five times with four different females, resulting in a total of 228 eggs in his mud nest, and M2 copulated at least three times with three different females, resulting in a total of 83 eggs. After the hatching of all nymphs inside his nest, M1 left the mud nest and established a new nesting site under a piece of tree fern trunk (Fig. 3). After 11 days, 54 eggs covered by debris (Fig. 4) and in two different stages of embryonic development (according to Machado et al. 2004) were found attached to the undersurface of the tree fern trunk. Since there was no egg under the tree fern trunk before M1 arrival, the presence of the clutch suggests that M1 copulated with two females or twice with the same female. M1 remained close to the eggs in the trunk nest until they hatched 16 days later.

Just before copulation, the male approached the female frontally and intensely tapped her genital opening with his second pair of legs. Meanwhile, the male also gently touched the dorsum of the female with his first pair of legs ($n = 2$). In one case, touching behavior lasted 30 s and, in the sequence, the male (M1) grasped the female pedipalps with his own pedipalps. The female raised the front of her body, exposing her ventral region to the genital opening of the male. In this position, the male everted his penis and penetrated the female's genital opening. The other courtship lasted almost 1 h and, during all this time, the male (M2) touched the female as described above. During most of the courtship, the female bent the front of her body so that it was impossible for the male to penetrate her. Occasionally, she also put her venter in contact with the substrate, also preventing the male from touching her genital opening. Eventually, the male managed to grasp the female pedipalps with his pedipalps and then she spontaneously raised the front of her body allowing penetration.

Both copulations lasted nearly 2 min, and during penetration, the male performed intense leg tapping on the dorsum of the female using his first pair of legs, and simultaneously on the female's hind legs and venter using his second pair of legs. Penetration was apparently terminated by the female when she was able to propel herself backwards with enough force to release herself from the grasp of the male's pedipalps. Immediately after separation, males continued to tap the dorsum and venter of their partners with the second pair of legs for nearly 2 min.

Oviposition.—After copulation, the female generally walked inside the mud nest for nearly 3 min ($n = 7$), always followed by the male, probably searching for a proper place for egg laying. In the first step of the oviposition, the female everted her ovipositor and placed its tip in contact with her chelicerae for up to 7 min. At the same time, the male, stood behind the female, repeatedly tapped her dorsum using his second pair of legs. Once every 3 min, the male also gently tapped the venter of the female ($n = 2$ ovipositions); it was not possible to see if the male touched the ovipositor. Next, the female released an egg, which was held on the chelicerae while she scraped the nest's wall with her first pair of legs (Fig. 1). Every two or three scrapes of the nest's wall, the female brought the leg to the mouth, probably to clean or humidify the tip of the leg; this process lasted from 7 to 13 min. In the sequence, the female put the egg on the scraped area using her chelicerae and rolled it on the substrate using the first pair of legs until the egg was completely covered by debris, a process that lasted up to 1 min (Fig. 2). After oviposition of each egg, the male walked around inside the nest until the female started to lay the next egg (Fig. 2). At this moment, the male resumed tapping the female using his second pair of legs, as described above. The whole process of oviposition lasted 2 to 4 days (mean \pm SD = 2.6 ± 0.7 ; $n = 8$), and was interrupted by periods of rest (sensu Elpino-Campos et al. 2001), when both male and female did not interact with each other. After this period, the female abandoned the nest and the eggs were left under the male protection until they hatched 23–24 days later. The mean number of eggs laid in each oviposition was 38.9 (SD = 12.2; $n = 8$), and the intervals between the two oviposition events of each female ranged from 9 to 12 days ($n = 8$).



Figures 3, 4.—3. Marked male of the harvestman *Chavesincola inexpectabilis* taking care of eggs laid on a piece of tree fern trunk. The dotted circles indicate the position of the eggs. 4. Detail of the clutch after the addition of more eggs. Note that the eggs are covered by debris (photos by B.A. Buzatto). Scale bars = 5 mm.

Paternal care.—Non-guarding males and females were frequently seen walking around in the terrarium at night, and they were observed eating at least 10 times. Guarding males, on the other hand, rarely left their nests to forage at night; when they did ($n = 2$), they remained within 10 cm of the nest entrance. Additionally, unlike females that ate the cockroach pieces on the spot, guarding males and males that

were defending mud nests without eggs took the food to their nests before consumption ($n = 6$). In one case, a non-guarding male was observed entering a mud nest and seemingly trying to remove some eggs with his pedipalps, probably as an attempt of cannibalism. The guarding male (M1), which was 2 cm away from the nest entrance, attacked the intruder male using the first pair of legs and pedipalps. The non-guarding male left the nest

without cannibalizing any egg, and was chased by the guarding male for nearly 30 s. After that, the guarding male returned to his nest and remained with the fourth pair of legs blocking the nest entrance for nearly one hour.

DISCUSSION

When males are in charge of egg brooding, they become a reproductive resource for females and some degree of sex-role reversal may be expected (Owens & Thompson 1994; Parker & Simmons 1996). In such cases, male-male competition may be less intense and no sexual dimorphism is expected. Although most gonyleptids show strong sexual dimorphism, males being larger and more armed than females, this dimorphism in paternal species of the subfamilies Caelopyginae and Progonyleptoidellinae is very subtle. Females of many species have spiny legs and apophyses as long as those of males (e.g., Pinto-da-Rocha 2002), or in other cases, neither sex has any leg armature at all (e.g., Kury & Pinto-da-Rocha 1997). However, strong sexual dimorphism may be found among paternal species of the subfamily Gonyleptinae. In this subfamily, males of some species defend very specific sites (holes in roadside banks and trunks) as nesting sites, and leg armature seems to be involved in the defense of this scarce resource against other males (Machado et al. 2004). Males of *C. inexpectabilis* also defend nesting sites and, as could be expected, males have strong armature on the fourth pair of legs. They use the spines and apophyses of these legs to fight other males and to repel them from the nesting sites. Similarly to males of *Neosadocus* sp., which also occupy holes in roadside banks as nesting sites (see figs. 2B, C in Machado et al. 2004), males of *C. inexpectabilis* use the heavily armed fourth pair of legs to block the entrance of their nests and to pinch intruder males.

Most descriptions of courtship in harvestmen of the suborder Laniatores lack detailed information, such as which parts of the female body are touched by the male. Even though the courtship behavior of *C. inexpectabilis* follows the general pattern previously recorded for some gonyleptid harvestmen (see Machado & Macías-Ordóñez 2007), here we provide additional information showing, for instance, that males intensively touch the genital opening of the female. It is possible that these touches stimulate the female to open her genital opening, a prerequisite for male intromission among Laniatores. Unreceptive females clearly avoid male touches on the genital opening by lowering the venter to the substrate. On the other hand, receptive females allow the males to grasp them with their pedipalps and raise the front of their bodies so that penetration can occur. The end of the copulation is also apparently determined by the females, when they are able to release themselves from the intromission and from the pedipalpal grasping. In species of Eupnoi, the female may reject intromission, but grasping seems harder to avoid because the male tightly hooks his long, sexually dimorphic pedipalps to the base of female's legs II near the trochanter. Apparently, Eupnoi males rely more on the powerful grasping to initiate copulation with females, whereas Laniatores rely more on precopulatory courtship (discussion in Machado & Macías-Ordóñez 2007).

Post-copulatory courtship in *C. inexpectabilis* occurs as males tap on the dorsum and venter of females using their legs. Intense

female stimulation both during and after copulation may be viewed as a male strategy to increase the number of eggs fertilized and also increase paternity (Eberhard 1996). Additionally, the total time spent by ovipositing females inside a male's nest may reach four days, quite a long period when compared to other harvestman species (e.g., Juberthie & Muñoz-Cuevas 1971; Mora 1990; Machado & Oliveira 1998; Willemart 2001). In *Pseudopucroliia* sp., another Heteropachylinae species we are studying in our laboratory, males block the entrance of the nest with their bodies and also actively prevent females from leaving (Nazareth & Machado unpub. data). This coercive behavior, associated with repeated copulations, is possibly another male strategy to increase paternity and the number of eggs that one female will lay inside the nest.

The oviposition behavior of *C. inexpectabilis* is markedly different from that of other Laniatores, including representatives of the family Gonyleptidae (e.g., Juberthie & Muñoz-Cuevas 1971; Machado & Oliveira 1998; Willemart 2001). A unique behavioral feature is that females hold the eggs on the chelicerae before depositing them on the substrate. It is possible that females use secretions from the mouthparts to cover the eggs before their deposition on the substrate to promote the attachment of debris on them or to moisten them with anti-pathogenic compounds, as some centipedes do (Brunhuber 1970; Lewis 1981). The behavior of covering eggs with debris has been previously described for several harvestman species of the families Cosmetidae and Gonyleptidae that present no care or exclusive maternal care (references in Willemart 2001). The only cases of egg covering reported so far for a paternal species occur in the tryaenonychids *Karamea* spp. (Machado 2007), which are not closely related to the Gonyleptidae (Giribet & Kury 2007). This behavioral trait, therefore, clearly evolved independently in these two families, but in both cases might be related to egg protection by providing camouflage and/or preventing dehydration (Willemart 2001; Elpino-Campos et al. 2001).

Maternal egg-guarding is a costly behavioral strategy for iteroparous arthropods because it reduces lifetime fecundity by increasing the risk of death from predation and reducing foraging opportunities for guarding females during the long periods of care (Tallamy & Brown 1999; see also Buzatto et al. 2007). Reduction of foraging is one of the main costs paid by guarding females and, according to the "enhanced fecundity hypothesis," exclusive post-zygotic paternal care may be viewed as a fitness-enhancing gift from males to females because it offers females two direct benefits: the cost-free care of their offspring and the freedom to forage for additional food (Tallamy 2001). After oviposition, eggs of *C. inexpectabilis* are left under the guard of the male, and females are released to forage and to produce more eggs. The intervals between two consecutive ovipositions ranged from 9 to 12 days, which is almost three times shorter than the interval between two ovipositions in the maternal gonyleptid *Discocyrtus oliverioi* Soares 1945, which was also studied in captivity where food was always available (Elpino-Campos et al. 2001; G. Machado, unpub. data). This interval is also 10–15 times shorter than the median interval between two ovipositions in three other maternal gonyleptids studied in the field (where food is supposed to be a limiting factor for female fecundity): *Bourguyia hamata* (Machado & Oliveira

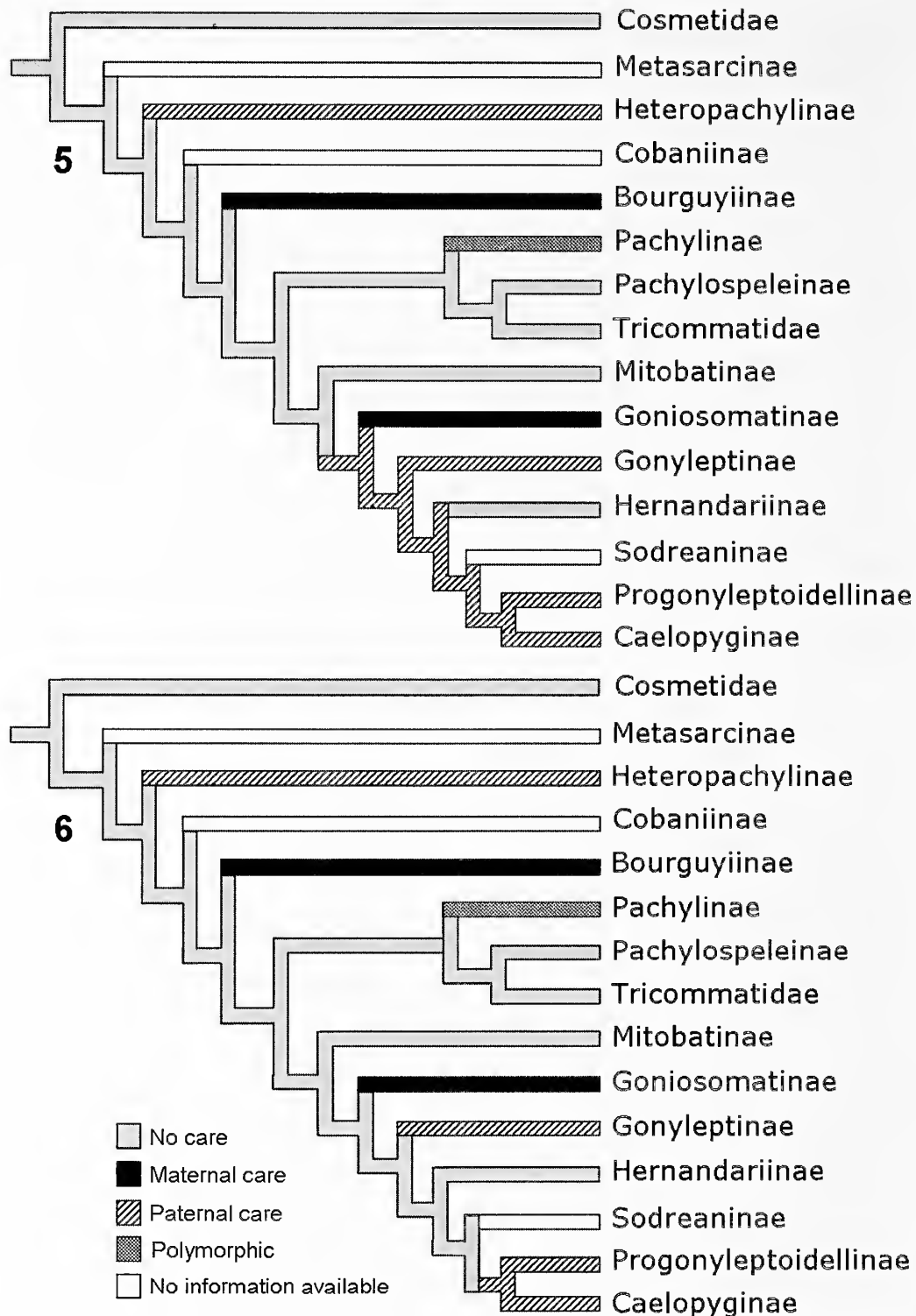


Figure 5, 6.—Internal phylogeny of the family Gonyleptidae (modified from Kury 1994 and Pinto-da-Rocha 2002) showing the forms of parental care presented by each subfamily. Behavioral data were mapped using the program Winelada (Nixon 1999), using ACCTRAN (5) and DELTRAN (6) optimization. Since there are no data on the internal phylogeny of some groups, the following assumptions were made: (1) most species of Cosmetidae do not care for the eggs (see table 12.2 in Machado & Macías-Ordóñez 2007) and the only case of maternal care reported so far in the family was considered as an autapomorphy (see Goodnight & Goodnight 1976 and Machado & Raimundo 2001); (2) although there is a great diversity in the forms of parental care within the subfamily Gonyleptinae (see table 12.2 in Machado & Macías-Ordóñez 2007), paternal care was tentatively considered as the plesiomorphic state in order to investigate how this polarity assumption could affect the optimization of this behavioral trait on the tree; (3) the information for the Pachylinae was considered as polymorphic because cases of no care and maternal care are evenly distributed in the species of this subfamily (see table 12.2 in Machado & Macías-Ordóñez 2007).

2002), *Goniosoma albiscryptum* (Willemart & Gnaspini 2004), and *Acutisoma proximum* (Buzatto et al. 2007). Apparently, the reproductive rate of *C. inexpectabilis* females is higher than females of species with maternal care, a likely consequence of their increased foraging rate, but experimental studies are necessary to address this question more carefully.

By mapping the available data about reproductive biology on the internal phylogeny of the Gonyleptidae, it is possible to infer that paternal care has evolved two or three times independently in the family, according to the type of optimization (Figs. 5, 6). Since the clutch and the nesting site of paternal species from the subfamilies Gonyleptinae and Progonyleptoidellinae + Caelopyginae are remarkably different (see discussion in Machado et al. 2004), we believe that DELTRAN optimization, which favors convergence, is the most appropriate scenario for the evolution of male care in the gonyleptids (Fig. 6). According to both Figs. 5 and 6, all cases of paternal care in gonyleptids are derived from no care. For the Heteropachylinae, however, this evolutionary transition should be interpreted cautiously because there is no published information on the reproductive biology of the Andean subfamily Metasarcinae and of the basal monotypic subfamily Cobaniinae. Data on the reproductive behavior of these two subfamilies are crucial to provide both a robust hypothesis about the plesiomorphic form of egg assistance in gonyleptids and a more complete scenario of the transitions between different forms of parental care in the family.

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LITERATURE CITED

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–265.
- Bhatkar, A. & W.H. Whitcomb. 1970. Artificial diet for rearing various species of ants. *Florida Entomologist* 53:229–232.
- Brunhuber, B.S. 1970. Egg laying, maternal care and development of young in the scolopendromorph centipede, *Cormocephalus anceps* Porat. *Zoological Journal of the Linnean Society* 49:225–234.
- Buzatto, B.A., G.S. Requena, E.G. Martins & G. Machado. 2007. Effects of maternal care on the lifetime reproductive success of females in a neotropical harvestman. *Journal of Animal Ecology* 76:937–945.
- Eberhard, W.G. 1996. *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton University Press, Princeton, New Jersey. 472 pp.
- Elpino-Campos, A., W. Pereira, K. Del-Claro & G. Machado. 2001. Behavioral repertory and notes on natural history of the neotropical harvestman *Discocyrtus oliverioi* (Opiliones: Gonyleptidae). *Bulletin of the British Arachnological Society* 12:144–150.
- Giribet, G. & A.B. Kury. 2007. Phylogeny and biogeography. Pp. 62–87. *In* *Harvestmen: the Biology of Opiliones*. (R. Pinto da Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.
- Goodnight, C.J. & M.L. Goodnight. 1976. Observations on the systematics, development and habits of *Erginulus clavotibialis* (Opiliones: Cosmetidae). *Transactions of the American Microscopical Society* 95:654–664.
- Juberthie, C. & A. Muñoz-Cuevas. 1971. Sur la ponte de *Pachylus quinamavidensis* (Opiliones, Gonyleptidae). *Bulletin de la Société d'histoire naturelle de Toulouse* 107:468–474.
- Kury, A.B. 1994. Early lineages of Gonyleptidae (Arachnida, Opiliones, Laniatores). *Tropical Zoology* 7:343–353.
- Kury, A.B. & R. Pinto-da-Rocha. 1997. Notes on the Brazilian harvestmen genera *Progonyleptoidellus* Piza and *Iporangaia* Mello-Leitão (Opiliones: Gonyleptidae). *Revista Brasileira de Entomologia* 41:109–115.
- Lewis, J.G.E. 1981. *The Biology of Centipedes*. Cambridge University Press, Cambridge, UK. 489 pp.
- Machado, G. 2007. Maternal or paternal egg guarding? Revisiting parental care in triaenonychid harvestmen (Opiliones). *Journal of Arachnology* 35:202–204.
- Machado, G. & R. Macías-Ordóñez. 2007. Reproduction. Pp. 414–454. *In* *Harvestmen: the Biology of Opiliones*. (R. Pinto da Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.
- Machado, G. & P.S. Oliveira. 1998. Reproductive biology of the Neotropical harvestman *Goniosoma longipes* (Arachnida: Opiliones: Gonyleptidae): mating and oviposition behaviour, brood mortality, and parental care. *Journal of Zoology* 246:359–367.
- Machado, G. & P.S. Oliveira. 2002. Maternal care in the neotropical harvestman *Bourguyia albiornata* (Arachnida, Opiliones): oviposition site selection and egg protection. *Behaviour* 139:1509–1524.
- Machado, G. & R.L.G. Raimundo. 2001. Parental investment and the evolution of subsocial behaviour in harvestmen (Arachnida: Opiliones). *Ethology Ecology and Evolution* 13:133–150.
- Machado, G., G.S. Requena, B.A. Buzatto, F. Osses & L.M. Rossetto. 2004. Five new cases of paternal care in harvestmen (Arachnida: Opiliones): implications for the evolution of male guarding in the Neotropical family Gonyleptidae. *Sociobiology* 44:577–598.
- Machado, G. & J. Warfel. 2006. First case of maternal care in the family Cranaidae (Opiliones: Laniatores). *Journal of Arachnology* 34:269–272.
- Macías-Ordóñez, R. 2000. Touchy harvestmen. *Natural History* 109:58–61.
- Martin, P. & P. Bateson. 1993. *Measuring Behaviour: An Introductory Guide*. Second edition. Cambridge University Press, New York. 222 pp.
- Mora, G. 1990. Parental care in a neotropical harvestman, *Zygopachylus albomarginis* (Arachnida: Gonyleptidae). *Animal Behaviour* 39:582–593.
- Nixon, K.C. 1999. Winclada (BETA) ver. 0.9.9. Published by the author, Ithaca, New York.
- Owens, I.P.E. & D.B.A. Thompson. 1994. Sex differences, sex ratios and sex roles. *Proceedings of the Royal Society B* 258:93–99.
- Parker, G. & L. Simmons. 1996. Parental investment and the control of sexual selection: predicting the direction of sexual competition. *Proceedings of the Royal Society B* 258:93–99.
- Pereira, W., A. Elpino-Campos, K. Del-Claro & G. Machado. 2004. Behavioral repertory of the Neotropical harvestman *Ilhaia cuspidata* (Opiliones, Gonyleptidae). *Journal of Arachnology* 32:22–30.
- Phillipson, J. 1959. The seasonal occurrence, life histories and fecundity of harvest-spiders (Phalangida, Arachnida) in neighborhood of Durham City. *Entomologist's Monthly Magazine* 95:134–138.

- Pinto-da-Rocha, R. 2002. Systematic review and cladistic analysis of the Caelopyginae (Opiliones, Gonyleptidae). *Arquivos de Zoologia* 36:357–464.
- Tallamy, D.W. 2001. Evolution of exclusive paternal care in arthropods. *Annual Review of Entomology* 46:139–165.
- Tallamy, D.W. & W.P. Brown. 1999. Semelparity and the evolution of maternal care in insects. *Animal Behaviour* 57:727–30.
- Tsurusaki, N. 1986. Parthenogenesis and geographic variation of sex ratio in two species of *Leiobunum* (Arachnida, Opiliones). *Zoological Science* 3:517–532.
- Willemart, R.H. 2001. Egg covering behavior of the neotropical harvestman *Promitobates ornatus* (Opiliones, Gonyleptidae). *Journal of Arachnology* 29:249–252.
- Willemart, R.H. & P. Gnaspini. 2004. Breeding biology of the cavernicolous harvestman *Goniosoma albiscriptum* (Arachnida, Opiliones, Laniatores): sites of oviposition, egg batches characteristics and subsocial behaviour. *Invertebrate Reproduction and Development* 45:15–28.
- Willemart, R.H., F. Osses, M.C. Chelini, R. Macías-Ordóñez & G. Machado. 2009. Sexually dimorphic legs in a neotropical harvestman (Arachnida, Opiliones): ornament or weapon? *Behavioral Processes* 80:51–59.

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Reversed cannibalism, foraging, and surface activities of *Allocosa alticeps* and *Allocosa brasiliensis*: two wolf spiders from coastal sand dunes

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Abstract. Environments where prey availability is scarce or highly variable have been reported as potential settings for the occurrence of paternal investment and sex-role reversal (choosy males and competitive, courting females). *Allocosa brasiliensis* (Petrunkévitch 1910) and *Allocosa alticeps* (Mello-Leitão 1944) are two sand-dwelling wolf spiders that construct burrows along the Uruguayan coastline. Both species present a reversal in typical sex roles and size dimorphism. In the present study, we investigated foraging behavior and population density of both species by performing monthly samplings at the field during one year. Both *Allocosa* are general and highly opportunistic predators, varying their diet according to prey availability. The three most represented common prey belonged to Araneae, Diptera, and Hymenoptera (Formicidae). There were high levels of cannibalism in *A. brasiliensis* and, furthermore, males were observed frequently preying on conspecific adult females. Our discussion of the results based on hypotheses about food limitation and sex-role reversal contributes to our understanding of *Allocosa* species and establishes them as models for future evolutionary, behavioral, and ecological studies.

Keywords: Lycosidae, Uruguay, prey, sex-role reversal, food limitation

Environments with fluctuations in prey abundance and access to refuges or other resources have been reported as potential causes for the evolution of paternal care and sex-role reversed systems (Gwynne 1991; Karlsson et al. 1997; Lorch 2002). *Allocosa brasiliensis* (Petrunkévitch 1910) and *Allocosa alticeps* (Mello-Leitão 1944) are two sympatric and synchronic wolf spider species that live in sandy coasts of Uruguay (Capocasale 1990; Costa 1995; Costa et al. 2006). Individuals reported in studies of Costa (1995), Simó et al. (2005), and Costa et al. (2006) as *Allocosa* sp. belong to *Allocosa alticeps*. The environment these *Allocosa* species inhabit can be considered harsh where prey abundance and weather conditions are highly variable. The changeable environment could be imposing unusual constraints on these species, affecting the sexual behavior of each gender and causing adaptations.

Recent studies (Aisenberg et al. 2007; Aisenberg & Costa 2008) report a reversal in typical sex-roles and size dimorphism for both spider species. Aisenberg & Costa (2008) reported that females are smaller than males, both in *A. brasiliensis* (carapace width, females: 4.63 ± 0.49 mm; males: 5.76 ± 0.59 mm) and *A. alticeps* (carapace width, females: 2.94 ± 0.30 mm; males: 3.28 ± 0.54 mm). The reproductive sexual peak of *A. brasiliensis* and *A. alticeps* takes place in January (Costa 1995; Costa et al. 2006). Females are the roving sexual aggressors that locate and court the males. Copulation takes place inside male burrows and after the final dismount, males abandon their burrows, leaving them to the females (Aisenberg et al. 2007; Aisenberg & Costa 2008).

Allocosa brasiliensis and *A. alticeps* are the sole wolf spiders adapted to living in the Uruguayan coastline (Costa et al. 2006). Food limitation could be an important factor affecting female and male feeding strategies in both lycosid species. Furthermore, occasional field observations suggested the occurrence of cannibalism of females by males of *A. brasiliensis* during the reproductive period (F.G. Costa and

A. Aisenberg, pers. obs.), a phenomenon considered unknown for spiders (Elgar 1992; Wise 2006). Both *Allocosa* species inhabit areas that have been drastically reduced in the last sixty years (Costa et al. 2006), possibly affecting population densities and competition for prey or other resources. In the present work, we studied feeding and surface activities of *A. brasiliensis* and *A. alticeps* with the hypotheses that both species are generalists with high levels of intraguild predation as adaptations for prey unpredictability and intraguild competition in these coastal habitats.

Foraging samplings took place over the course of 11 mo (June 2007–April 2008) in the coastal sand dunes of Marindia ($34^{\circ}46'52.3''\text{S}$, $55^{\circ}49'29.6''\text{W}$), Salinas ($34^{\circ}46'59.8''\text{S}$, $55^{\circ}49'51.5''\text{W}$), Canelones, and Paso del Molino ($34^{\circ}16'40.10''\text{S}$, $55^{\circ}14'00.80''\text{W}$), Lavalleja, Uruguay. For 1 h after dark, four to six researchers using headlamps collected *Allocosa* spiders and any prey they had captured. Feeding spiders and prey were captured and taken to the laboratory for identification. Prey were identified to family, and in the case of Araneae and Hymenoptera, to genus. We considered any prey that was primarily consumed so that identification was unfeasible as “unidentified prey.”

Surface activity was studied monthly in Salinas from June 2004 to April 2005, for 2 h after dark, using headlamps. We considered the presence of *Allocosa* individuals walking as an event of activity. We labeled as “sea-side” the side of the dune which faced the sea-front; the opposite side was designated as “land-side.” Spiders were sampled in four plots of $5 \text{ m} \times 5 \text{ m}$ (two plots on the sea-side and two on the land-side) that were drawn parallel to the line of the coast, on the first line of dunes. Additionally, in the period between December 2004 and April 2005, we recorded surface activity as reported previously and related it to the presence/absence of vegetation on the plot. We identified and sexed the individuals in the field. Voucher specimens of both species were deposited in the

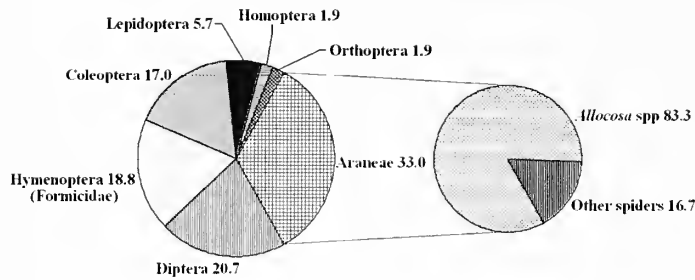


Figure 1.—Prey captured by individuals of both *Allocosa* species, with the corresponding percentages ($n = 50$).

arachnological collection of Sección Entomología, Facultad de Ciencias, Montevideo, Uruguay.

We recorded 45 individuals of *A. brasiliensis* and 9 individuals of *A. alticeps* feeding during the sampling periods. Most of the diet consisted of spiders, represented mainly by other *Allocosa* individuals. *Allocosa* spiders also preyed on Diptera, Hymenoptera, Coleoptera, Lepidoptera, Homoptera, and Orthoptera individuals but in lower frequencies (Fig. 1). The Hymenoptera captured were worker *Acromyrmex* and *Dorymyrmex* ants, caught on their trails. We found a high rate of intraguild predation in *A. brasiliensis* (Fig. 2). Surprisingly, though females and large juveniles of *A. brasiliensis* preyed on small conspecific juveniles and on adults or juveniles of *A. alticeps*, adult males of *A. brasiliensis* preyed frequently on females of their own species (Fig. 2).

We observed 37 *Allocosa* individuals on the land-side of the dunes and 9 on the sea-side. Surface activity and prey capture showed higher values between December and January, while a lower intensity of feeding was registered in the period between June and November (Fig. 3). We found 13 individuals of *A. brasiliensis* in areas without vegetation and 5 in areas with vegetation. *Allocosa alticeps* did not show preference for areas with ($n = 9$) or without vegetation ($n = 6$).

The present results indicate that the diets of both *Allocosa* species are non-specific and highly opportunistic, according to prey availability. The occurrence of the three most represented prey (Araneae, Diptera, and Hymenoptera) was highly variable through the year. Both Diptera and Hymenoptera individuals were frequently caught by *Allocosa* spiders during their nuptial swarms or, in the case of ants, while working on

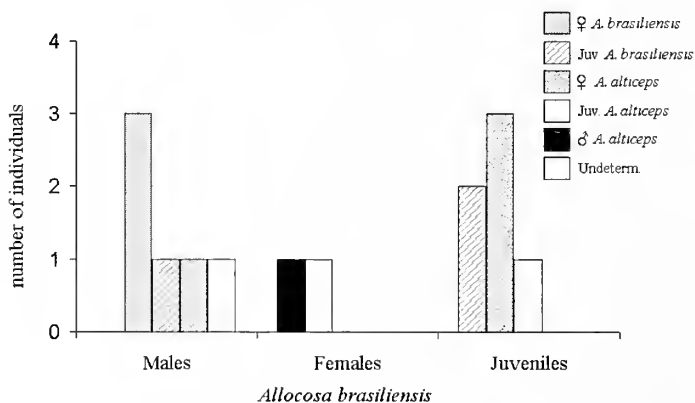


Figure 2.—Number of males, females, and juveniles of *A. brasiliensis* found feeding on individuals of *A. alticeps*, or individuals from their own species.

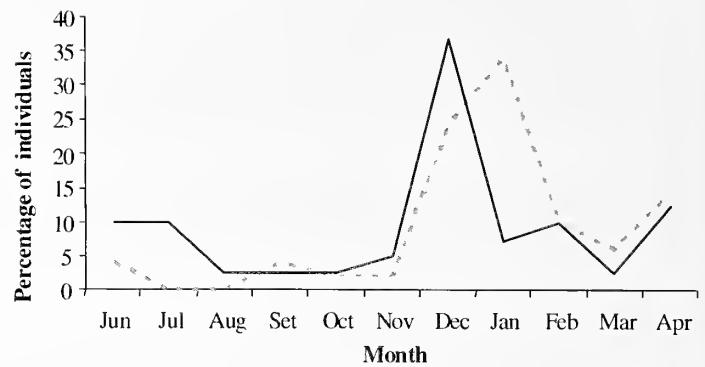


Figure 3.—Phenology of prey capture (dotted line) and surface activity (black line) recorded for both *Allocosa* species (individuals foraging $n = 50$; individuals walking $n = 213$).

their characteristic trails. The consumption of ants in natural conditions has been cited for web-building spiders, consisting mainly of winged ants but also walking individuals (Carico 1978; Nentwig 1987). Ground-hunting salticids, thomisids, gnaphosids, and oxyopids often show a high percentage of ants in their diets (Nentwig 1987; Foelix 1996) and members of the Zodariidae family are myrmecophages (Foelix 1996; Pékar 2004; Pékar et al. 2008). Moya-Laraño & Wise (2007) reported *Schizocosa* spiders (Lycosidae) feeding on ants under laboratory conditions. However, studies on lycosid spiders in the field report that Collembola, Diptera, Cicadina, Aphidina, and Araneae would be the main prey groups for this family (Nentwig 1987). Moya-Laraño et al. (2002) provide a different list of prey (absence of ants) for *Lycosa tarentula*, another burrowing wolf spider. Ants are considered very abundant in coastal areas, especially during the summer (Costa et al. 2006) and though they can be considered small prey for a spider the size of an *Allocosa*, they are the most predictable prey. The consumption of ants by *Allocosa* spiders could suggest food limitation and the requirement of special adaptations to manage potentially dangerous prey.

The lack of cannibalism and feeding on small prey in *A. alticeps* could be associated with a smaller size and, consequently, lower energetic requirements (Andersson 1994; Blanckenhorn 2005; Foellmer & Fairbairn 2005). On the other hand, cannibalism rates are high in *A. brasiliensis*. Intraguild predation is considered widespread among wolf spiders (Fernandez-Montraveta & Ortega 1990; Wagner & Wise 1996; Moya-Laraño et al. 2002). In general, studies report juveniles feeding on other juveniles, adults feeding on juveniles, or females feeding on males; overall large individuals feed on small ones (Polis 1981; Polis et al. 1989, 1997; Wise 2006). However, we found males of *A. brasiliensis* cannibalizing females of the same species, a phenomenon unexpected for spiders (Elgar 1998; Elgar & Schneider 2004; Wise 2006). Although we observed males cannibalizing females in just three instances (see Fig. 2), this fact is remarkable because observations of this kind in the field are very scarce even in studies with substantial field effort (Moya-Laraño et al. 2002). The consumption of females by male spiders can be considered non-adaptive, in general, in terms of losing a potential mate. Males of *A. brasiliensis* are sedentary, probably remaining inside their burrows without feeding for long periods (Costa et al. 2006; Aisenberg et al. 2007). So, after copulation and

before constructing a new burrow, they need to forage intensively. Considering the high concentration of *Allocosa* individuals in some areas and the fact that copulations take place exclusively inside male burrows (Aisenberg et al. 2007), females could turn into a good meal for a hungry and large recently-copulated male without a burrow. This would mean no risks to male paternity, as copulated females stay inside the burrows after copulation and until the emergence of spiderlings (Aisenberg et al. 2007). The cannibalism level increases with increasing size-differences (Polis 1981; Polis et al. 1989, 1997; Elgar 1998; Buddle et al. 2003; Wise 2006), so the larger size in *Allocosa* males compared to females could be favoring this atypical male strategy. Furthermore, males of sex-role reversed species are expected to be choosy (Gwynne 1991; Andersson 1994). Male selection with regard to female size has been cited in *Lycosa tarantula* (L. 1758), another role reversed wolf spider species (Moya-Laraño et al. 2003; Huber 2005). Males of *A. brasiliensis* could exhibit extreme mate choice based on female reproductive or nutritional status: copulate with the female or eat her (Elgar 1992). Adaptive foraging (Newman & Elgar 1991), mistaken identity (Gould 1984), and aggressive-spillover (Arnqvist & Henriksson 1997) hypotheses, already tested in other spider species, require further testing in *A. brasiliensis*.

A. brasiliensis was more highly represented in our samplings compared with *A. alticeps*. This could mean that the first species is more abundant, in contrast to the findings of Costa et al. (2006) based on results of pitfall trapping in the same areas, or the fact that it is less sedentary. Furthermore, *A. brasiliensis* individuals could be more easily detected due to their larger size or their greater presence in more open areas compared with *A. alticeps*. However, present surface activity data needs more exhaustive field work, recording not only surface activity but also burrow density, presence of individuals inside open / closed burrows and marking - tracking of individuals.

In the last century, the coastal landscape of the Río de la Plata and Atlantic Ocean in Southern Uruguay has decreased considerably, especially due to urbanization (Costa et al. 2006). Simó et al. (2005) reported the occurrence of *Allocosa* spiders strictly associated with the presence of sand dunes. The current results suggest that the highest surface and foraging activities of both *Allocosa* spiders coincide with the summer of the Southern hemisphere. During this season, coastal areas are most critically affected by tourism, which could also be impacting negatively on critical phases of the spiders' life cycle. This fact may be considered for adequate management plans for these areas. Simó et al. (2005) also postulated *Allocosa* species as potential biological indicators of human effects on coastal ecosystems, as Marshall et al. (2000) did for *Geolycosa*, another burrowing wolf spider species of coastal areas. Both *Allocosa* species seem to be more abundant on the land-side of the dunes, probably because these areas are more protected against the strong winds typical of the Uruguayan coastline. On the other hand, the burrows of the sea-side could be closed off by the spiders due to the strong wind beating on this side of the dune, thus escaping observers' detection. This behavior has been reported for another wolf spider inhabitant of coastal sand dunes (Gwynne & Watkiss 1975). *Allocosa brasiliensis* seems to be more closely associated with areas

without vegetation compared to *A. alticeps*, though we need further studies to confirm the trend. Marshall (1997) reported that *Geolycosa xera arboldi* McCrone 1963, another burrowing wolf spider inhabitant from sand dunes, was more directly associated with areas without vegetation. In the first decades of the twentieth century, dunes of the Uruguayan coast were fixed by human plantation of exotic vegetation as *Acacia longifolia*, *Pinus* spp. and *Eucaliptus* spp., especially on the land-side of the dunes (Costa 1995). Areas with exotic vegetation are associated with invader spider species, so the exclusion of *A. brasiliensis* from these areas could be a mechanism to avoid competition for resources, interference competition, and intraguild predation. Their significance as models for testing sex-role constraints in spiders and their potential as biological indicators make *A. brasiliensis* and *A. alticeps* good candidates for further studies that will make clear the effects of environmental factors on the inhabitants of coastal sand dunes and thus contribute to adequate management plans for these areas.

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LITERATURE CITED

- Aisenberg, A. & F.G. Costa. 2008. Reproductive isolation and sex role reversal in two sympatric sand-dwelling wolf spiders of the genus *Allocosa*. *Canadian Journal of Zoology* 86:648–658.
- Aisenberg, A., C. Viera & F.G. Costa. 2007. Daring females, devoted males, and reversed sexual size dimorphism in the sand-dwelling spider *Allocosa brasiliensis* (Araneae, Lycosidae). *Behavioral Ecology and Sociobiology* 62:29–35.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, New Jersey. 599 pp.
- Arnqvist, G. & S. Henriksson. 1997. Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evolutionary Ecology* 11:255–273.
- Blanckenhorn, W.U. 2005. Behavioral causes and consequences of sexual size dimorphism. *Ethology* 111:977–1016.
- Buddle, C.M., S.E. Walker & A.L. Rypstra. 2003. Cannibalism and density-dependent mortality in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). *Canadian Journal of Zoology* 81:1293–1297.
- Capocasale, R.M. 1990. Las especies de la subfamilia Hipassinae de América del Sur (Araneae, Lycosidae). *Journal of Arachnology* 18:131–141.
- Carico, J.E. 1978. Predatory behavior in *Euryopis funebris* (Hentz) (Araneae: Theridiidae) and the evolutionary significance of web reduction. Pp. 51–58. *In* *Arachnology*. (P. Merrett, ed.). Symposia of the Zoological Society of London. Volume 42. Academic Press, London.
- Costa, F.G. 1995. Ecología y actividad diaria de las arañas de la arena *Allocosa* spp. (Araneae, Lycosidae) en Marindia, localidad costera del sur del Uruguay. *Revista Brasileira de Biologia* 55:457–466.

- Costa, F.G., M. Simó & A. Aisenberg. 2006. Composición y ecología de la fauna epigea de Marindia (Canelones, Uruguay) con especial énfasis en las arañas: un estudio de dos años con trampas de intercepción. Pp. 427–436. *In* Bases para la conservación y el manejo de la costa uruguaya. (R. Menafrá, L. Rodríguez-Gallego, F. Scarabino & D. Conde, eds.). Vida Silvestre Uruguay, Montevideo. Pp. 668.
- Elgar, M.A. 1992. Sexual cannibalism in spiders and other invertebrates. Pp. 128–155. *In* Cannibalism Ecology and Evolution Among Diverse Taxa. (M.A. Elgar & B.J. Crespi, eds.). Oxford University Press, Oxford, UK.
- Elgar, M.A. 1998. Sperm competition and sexual selection in spiders and other arachnids. Pp. 307–339. *In* Sperm Competition and Sexual Selection. (T.R. Birkhead & A.P. Möller, eds.). Academic Press, London.
- Elgar, M.A. & J.M. Schneider. 2004. Evolutionary significance of sexual cannibalism. *Advances in the Study of Behaviour* 34:135–163.
- Fernández-Montraveta, C. & J. Ortega. 1990. El comportamiento agonístico de hembras adultas de *Lycosa tarentula fasciventris* (Araneae, Lycosidae). *Journal of Arachnology* 18:49–58.
- Foelix, R.F. 1996. *Biology of Spiders*, Second edition. Oxford University Press, New York. 330 pp.
- Foellmer, M.W. & D.J. Fairbairn. 2005. Selection on male size, leg length and condition during mate search in a sexually highly dimorphic orb-weaving spider. *Oecologia* 142:653–662.
- Gould, S.J. 1984. Only his wings remained. *Natural History* 93(9): 10–18.
- Gwynne, D.T. 1991. Sexual competition among females: what causes courtship-role reversal? *Trends in Ecology and Evolution* 6:118–121.
- Gwynne, D.T. & J. Watkiss. 1975. Burrow-blocking behavior in *Geolycosa wrightii* (Araneae, Lycosidae). *Animal Behaviour* 23:953–956.
- Huber, B.A. 2005. Sexual selection research on spiders: progress and biases. *Biological Reviews* 80:363–385.
- Karlsson, B., O. Leimar & C. Wiklund. 1997. Unpredictable environments, nuptial gifts and the evolution of size dimorphism in insects: an experiment. *Proceedings of the Royal Society of London B* 264:475–479.
- Lorch, P. 2002. Understanding reversals in the relative strength of sexual selection on males and females: a role for sperm competition? *American Naturalist* 6:645–657.
- Marshall, S.D. 1997. The ecological determinants of space use by a burrowing wolf spider in a xeric shrubland ecosystem. *Journal of Arid Environments* 37:379–393.
- Marshall, S.D., W.R. Hoeh & M.A. Deyrup. 2000. Biogeography and conservation biology of Florida's *Geolycosa* wolf spiders: threatened spiders in endangered ecosystems. *Journal of Insect Conservation* 4:11–21.
- Moya-Laraño, J., J.M. Orta-Ocaña, J.A. Barrientos, C. Bach & D.H. Wise. 2002. Territoriality in a cannibalistic burrowing wolf spider. *Ecology* 83:356–361.
- Moya-Laraño, J., J. Pascual & D.H. Wise. 2003. Mating patterns in late-maturing female Mediterranean tarantulas may reflect the cost and benefits of sexual cannibalism. *Animal Behaviour* 66:469–476.
- Moya-Laraño, J. & D.H. Wise. 2007. Direct and indirect effects of ants on a forest-floor food web. *Ecology* 88:1454–1465.
- Nentwig, W. 1987. The prey of spiders. Pp. 249–263. *In* *Ecophysiology of Spiders*. (W. Nentwig, ed.). Springer-Verlag, Berlin.
- Newman, J.A. & M.A. Elgar. 1991. Sexual cannibalism in orb-weaving spiders: an economic model. *American Naturalist* 138:1372–1395.
- Pekár, S. 2004. Predatory behavior of two European ant-eating spiders (Araneae, Zodariidae). *Journal of Arachnology* 32:31–41.
- Pekár, S., S. Toft, M. Hrušková & D. Mayntz. 2008. Dietary and prey-capture adaptations by which *Zodariion germanicum*, an ant-eating spider (Araneae: Zodariidae), specialises on the Formicinae. *Naturwissenschaften* 95:233–239.
- Polis, G.A. 1981. The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics* 12:225–251.
- Polis, G.A., W.B. Anderson & R.D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Polis, G.A., C.A. Myers & R.D. Holt. 1989. The ecology and evolution of intraguild predation. Potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297–330.
- Simó, M., J. Coll, M. Viglioni & A. Laborda. 2005. Actividad, distribución espacial y fragmentación del hábitat en dos especies de *Allocosa* Banks, de la costa sur del Uruguay (Araneae, Lycosidae). *Actas de resúmenes, Primer Congreso Latinoamericano de Aracnología*, 148 pp.
- Wagner, J.D. & D.H. Wise. 1996. Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. *Ecology* 77:639–652.
- Wise, D.H. 2006. Cannibalism, food limitation, intraspecific competition, and the regulation of spider copulations. *Annual Review of Entomology* 51:441–465.

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Phenology of Opiliones on an altitudinal gradient on Lefka Ori Mountains, Crete, Greece

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Abstract. The harvestman fauna was studied along an altitudinal gradient on the southern slope of Lefka Ori Mountains, Crete, Greece for one year. Four sampling areas were defined at 800, 1200, 1600, and 2000 m elevation and they were sampled with pitfall traps that were emptied at monthly intervals. In total, six species were collected: *Histicostoma creticum* (Roewer 1927), *Lacinius insularis* Roewer 1923, *Graecophalangium cretaeum* Martens 1966, *Opilio insulae* Roewer 1956, *Rafalskia cretica* (Roewer 1923) and *Leiobunum ghigii* Di Caporiacco 1929. Species richness was the same (5 spp.) at the three lower zones and then declined to three species at 2000 m. Catches were more than double at this elevation. Differences of phenological patterns were observed among species and among altitudinal zones within the same species. High activity during spring and autumn and a summer recession were characteristic of most taxa. Opiliones did not seem strongly affected by the severe harshness of climatic conditions at higher elevations, as observed in other taxa, indicating a strong physiological tolerance and/or behavioral adaptation in order to withstand environmental stress.

Keywords: Elevation, harvestmen, Mediterranean, pitfall traps, seasonal variation

Mountain ecology has long been the focus of interest for many plant and animal ecologists. Mani (1968) compiled the earlier entomological literature of the alpine zone, which consists mainly of anecdotal, casual, or incidental observations. The lack of knowledge on quantitative and functional aspects of the soil fauna of Mediterranean-type ecosystems has been noted by Di Castri & Vitali-Di Castri (1981). However an effort has been made to try to clarify patterns of ecological variation in this kind of ecosystems in Greece. Stamou et al. (1984) studied the soil macrofauna succession in Mt. Olympus and Legakis (1986) analyzed the arthropod soil fauna of Mt. Hymettos. Despite their contribution to the knowledge of ecological variation of the fauna in Mediterranean-type ecosystems, these studies covered few taxonomic groups and did not account for seasonal variation of the fauna. Sfenthourakis (1992) gave a clearer picture of the variation of isopod assemblages along altitudinal gradients in three mountain systems of Greece. Lymberakis et al. (2003) discussed the altitudinal variation of Oniscidean communities and Chatzaki et al. (2005a) presented the variation of spider communities along altitudinal gradients on the island of Crete, Greece, as far as both composition and activity on a year-long basis are concerned. The phenology of the same group is presented in a separate paper (Chatzaki et al. 2005b).

Studies on the Opiliones of Crete have been predominantly faunistic and taxonomic. Only the work of Martens (1966) contains some phenological and chorological notes concerning the opilionid fauna of the island. As a whole, publications about the biology, ecology, and zoogeography of the group on Crete are lacking.

In view of this, the present paper is the first that concentrates on the comparison of the phenology of Opiliones at different elevations, as well as on the seasonal and altitudinal variation in species composition in Lefka Ori

(White Mountains) on Crete. Lefka Ori is one of the most important insular mountain systems of the Mediterranean region, because of its high elevations, the large area it covers and its unique topography and climate (see climate paragraph in Methods).

The results presented here may serve as a basis for further comparison of the phenological peculiarities of the Opiliones in the region, as well as for the evaluation and analysis of the adaptive strategies of the endemics and their related species in other parts of the Balkan Peninsula.

METHODS

Description of the study area.—The Lefka Ori mountain system, situated at the western part of the island, is the most massive mountain range of Crete, including 56 peaks over 2000 m, the highest of which reaches an elevation of 2453 m. The study was carried out on the southern slope of Lefka Ori, just above the plateau of Anopolis found at ca 600 m (Fig. 1). Four sampling sites were selected, according to the main vegetation types, along the altitudinal gradient from 800 m to 2000 m:

1. An old mature forest of *Pinus brutia* Ten. at 800 m above sea level (a.s.l.) (35°14'N, 24°5'E), with very little understory, consisting mainly of *Quercus coccifera* L. shrubs and phrygana species, such as *Euphorbia acanthothamnus* Heldr. & Sart. ex Boiss., *Sarcopoterium spinosum* (L.), *Verbascum spinosum* L. and *Drimia maritima* (L.).
2. A *Cupressus sempervirens* L. mature forest at 1200 m a.s.l. (35°15'N, 24°6'E), composed mainly of *Cupressus sempervirens*, *Quercus coccifera* and a few *Acer sempervirens* L. trees. The understory is practically absent in this vegetation type.
3. A plateau immediately over the timberline at 1600 m a.s.l. (35°16'N, 24°5'E), partially covered with crawling

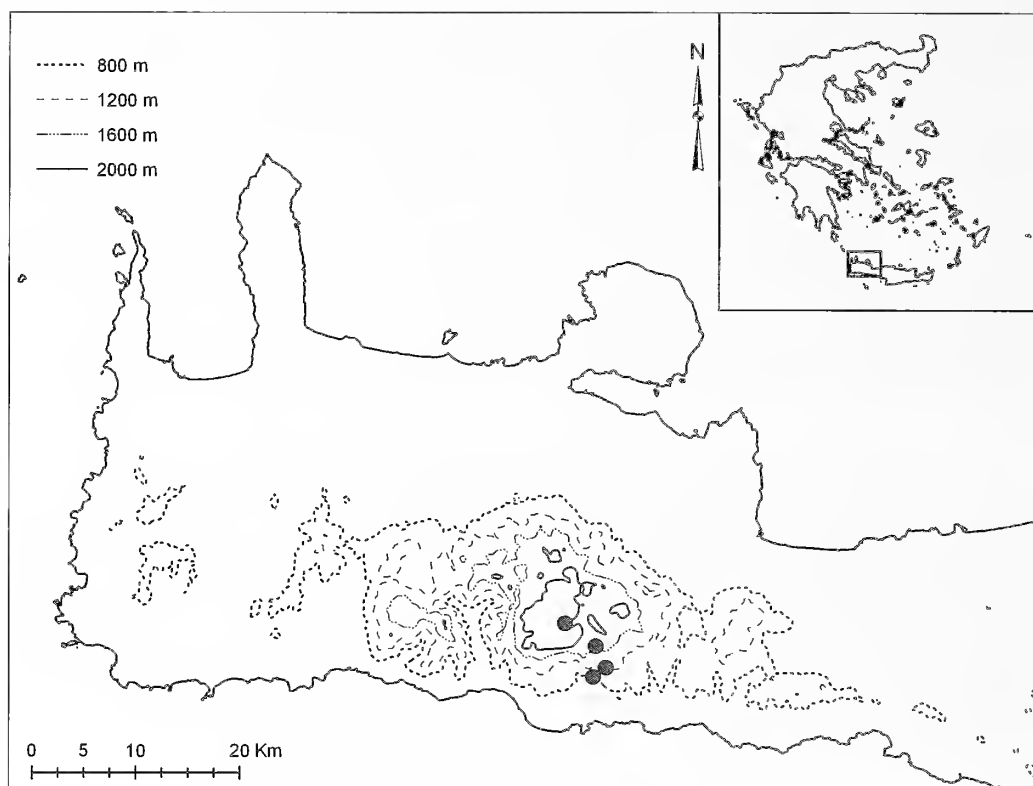


Figure 1.—Western end of Crete with collection sites. Inset: Greece.

scrubs of *Juniperus oxycedrus* L. subsp. *oxycedrus* and *Berberis cretica* L., accompanied by *Prunus prostrata* Labill., *Rhamnus saxatilis* Jacq. subsp. *prunifolia* (Sm), *Acantholimon ulicinum* (Willd. ex Schult.), *Satureja spinosa* L. and *Anchusa caespitosa* Lam.

4. A rocky site at 2000 m a.s.l. (35°17'N, 24°3'E), where the dominant scrub plants are: *Berberis cretica*, *Prunus prostrata*, *Astragalus angustifolius* Lam., and *Satureja spinosa*. Plants are largely restricted to areas offering wind shelter.

The area, as the whole of the island, is a karstic landscape. The ground is largely covered by stones and rocks that provide shelters for ground living animals. Human presence in the area dates from antiquity. For the last two centuries, but especially at present, intense grazing by sheep and goats takes place over the entire area. A main effect of overgrazing and the consequent trampling of the soil is that densities of most arthropod taxa have been reduced (Legakis 1986).

Climate.—The climate of Crete is typical Mediterranean with 5–7 mo of arid, hot and dry summers, alternating with shorter periods of rainy, mild winters. There are not sufficient meteorological data, especially for the high mountains. Mean annual temperatures fall 6° C per 1000 m rise in elevation (Grove et al. 1991). The range of temperatures is much narrower near the coast than in the mountains, due to the more maritime character of the former (Strid et al. 1995). Although there are no records of the precipitation above 900 m, Rackham & Moody (1996) estimated that at the top of Lefka Ori the annual precipitation must be as high as 2000 mm. In southern Lefka Ori, snow above 1400 m can be

several meters high, but the water disappears into the porous crystalline limestone immediately after the snow melts in May. Bonnefont (1972) estimated that snow cover lasts in Crete for 2–3 mo at 1500 m and for 5–6 mo at 2000 m. Over 2000 m, the snow cover lasts generally from November to May and then melts progressively. Small, localized spots can persist until August. During the summer months, the lower atmospheric pressure and the lack of trees combined with other physical characteristics (strong winds, thin soils, large proportion of precipitation as snow), favor high insolation and create dry and hot conditions (Shanks 1956; Mani 1990). This harsh landscape (because of snow cover in winter and high aridity in summer) forms the “High Desert” of the Lefka Ori highlands, a term coined by Rackham & Moody (1996) to describe a unique environment that does not exist to such extreme in any other Mediterranean mountain.

Sampling.—Harvestmen were collected by pitfall trapping. Forty plastic cups (10 cm depth × 7 cm diam.) were used per site. Though these dimensions are rather small, traps were capable of catching large arthropods (scorpions, large spiders, centipedes), and even lizards. Traps were placed in a straight-line ca 3 m apart. Undiluted ethylene glycol was used as a preservative. To diminish passive filling of the traps with organic matter and water, as well as predation from larger animals and vandalism, they were partially covered with stones, without reducing access to them by the animals. Traps were emptied at approximately 30-day intervals from August 1990 to March 1992. However, the results presented here include data from one full collecting year (March 1991 to February 1992), since data from the other years did not deviate from the results obtained from the main collecting

Table 1.—Species overall presence and total activity (transformed into number of individuals per 100 trap-days) at different elevations of Lefka Ori Mountain, Crete.

Species	Elevation			
	800 m	1200 m	1600 m	2000 m
<i>Lacinius insularis</i>	2.82		21.06	31.94
<i>Opilio insulae</i>	6.48	20.97	6.56	32.10
<i>Graecophalangium cretaeum</i>	4.32	5.73	6.01	9.70
<i>Rafalskia cretica</i>	13.00	6.53	0.84	
<i>Histicostoma creticum</i>	0.36	0.16		
<i>Leiobunum ghigii</i>		1.27	0.26	
Total	26.98	34.66	34.73	73.74

year. In the phenology graphs the last two months are presented jointly (J–F) because there was no intermediate emptying of the traps.

Data analysis.—Opiliones were identified by P. Mitov. Vouchers are deposited at the Natural History Museum of the University of Crete and some are kept in the private collection of P. Mitov.

As some traps were destroyed or the number of collecting days per sampling period was not equal, sampling effort was unequal too. In order to render the data from four sites and eleven sampling periods comparable, catches from each sample were transformed into catches per 100 trap-days.

RESULTS

Descriptive analysis and correlation.—Six species, belonging to the families Phalangidae (4 spp.), Nemastomatidae (1 sp.) and Sclerosomatidae (1 sp.) and represented by 2226 specimens were collected. Species are: *Histicostoma creticum* (Roewer 1927), *Lacinius insularis* Roewer 1923, *Graecophalangium cretaeum* Martens 1966, *Opilio insulae* Roewer 1956, *Rafalskia cretica* (Roewer 1923) (= *Metaplatybinus rhodiensis* Roewer 1924), and *Leiobunum ghigii* Di Caporiacco 1929. The latter is recorded from Crete for the first time. Two out of the three species that reach the elevation of 2000 m—*L. insularis* and *G. cretaeum*—are endemic to the island. All other species may be characterized as Ponto-Mediterranean faunistic elements (sensu De Lattin 1949, 1967).

Species overall presence and total catches at the study sites are presented in Table 1. The number of species is five at the three lower elevations and decreases to three at 2000 m. Species overall catches increase gradually from 800 to 1600 m and become highest (more than double) at 2000 m. The qualitative and quantitative composition among the first three elevations is different.

Lacinius insularis presents statistically significant positive correlation with elevation (Pearson's coefficient $R = 0.378$, $P = 0.03$), while *Rafalskia cretica* presents significant negative correlation with increasing elevation (Pearson's coefficient $R = -0.396$, $P = 0.023$). The remaining species do not present any significant correlation with elevation.

Phenology.—The phenology of the dominant species at each site is presented in Figs. 2–5. *Lacinius insularis* was absent at the 1200 m site. Since its total catches seem to significantly increase at the two higher elevations (Table 1, Fig. 2) and sampling was equally intense at all sites, its absence from 1200 m cannot be accidental. At the other elevation, *L.*

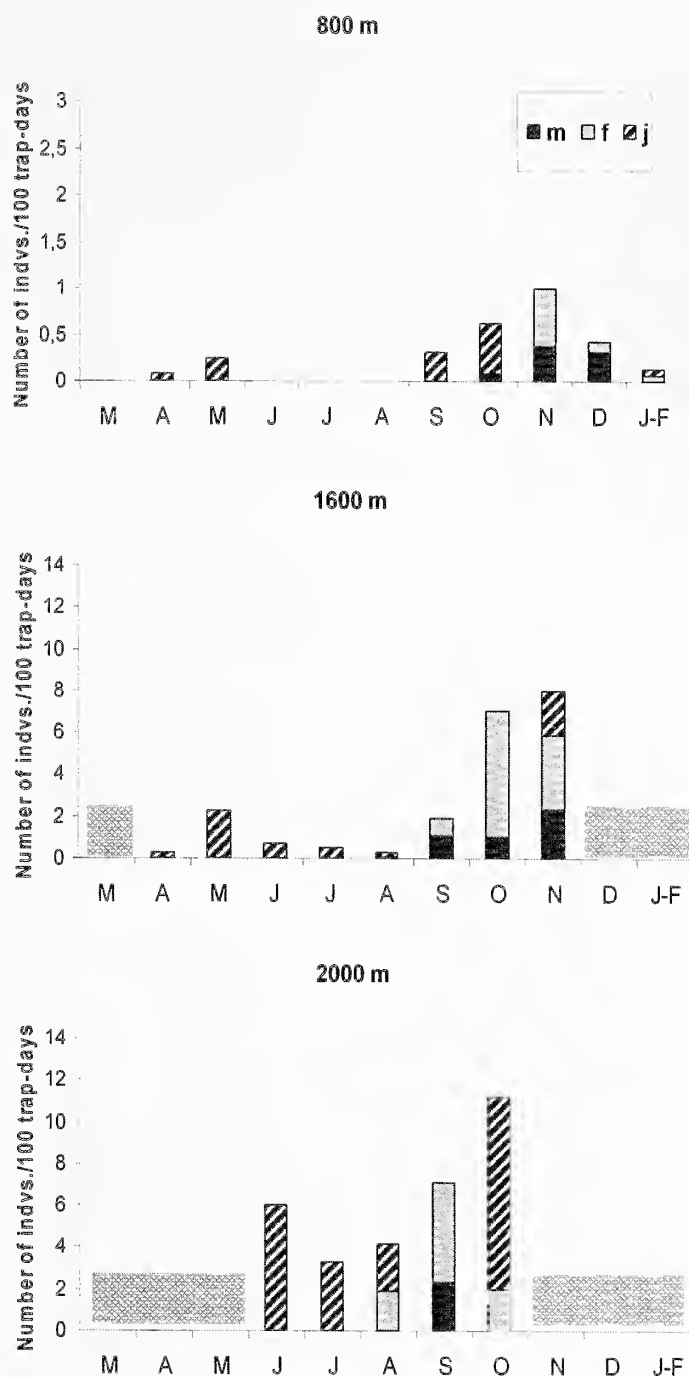


Figure 2.—Phenology of males (m), females (f) and juveniles (j) of *L. insularis* at different elevations. Grey horizontal bars indicate the months during which the sites were covered by snow.

insularis shows one peak of activity in autumn, represented mainly by female individuals. This peak is shifted from November at 800 m to September at 2000 m, thus the peak of activity occurs one month earlier at each higher altitudinal zone. Juveniles become mainly active in late spring (May at 800 m and 1600 m) and then again in autumn (September–October at 800 m and November at 1600 m). At the 2000 m site juveniles become very active in June and then again in October. This probably means that individuals of this species hibernate as immatures and remain inactive for a longer period, until the following summer when they mature (August)

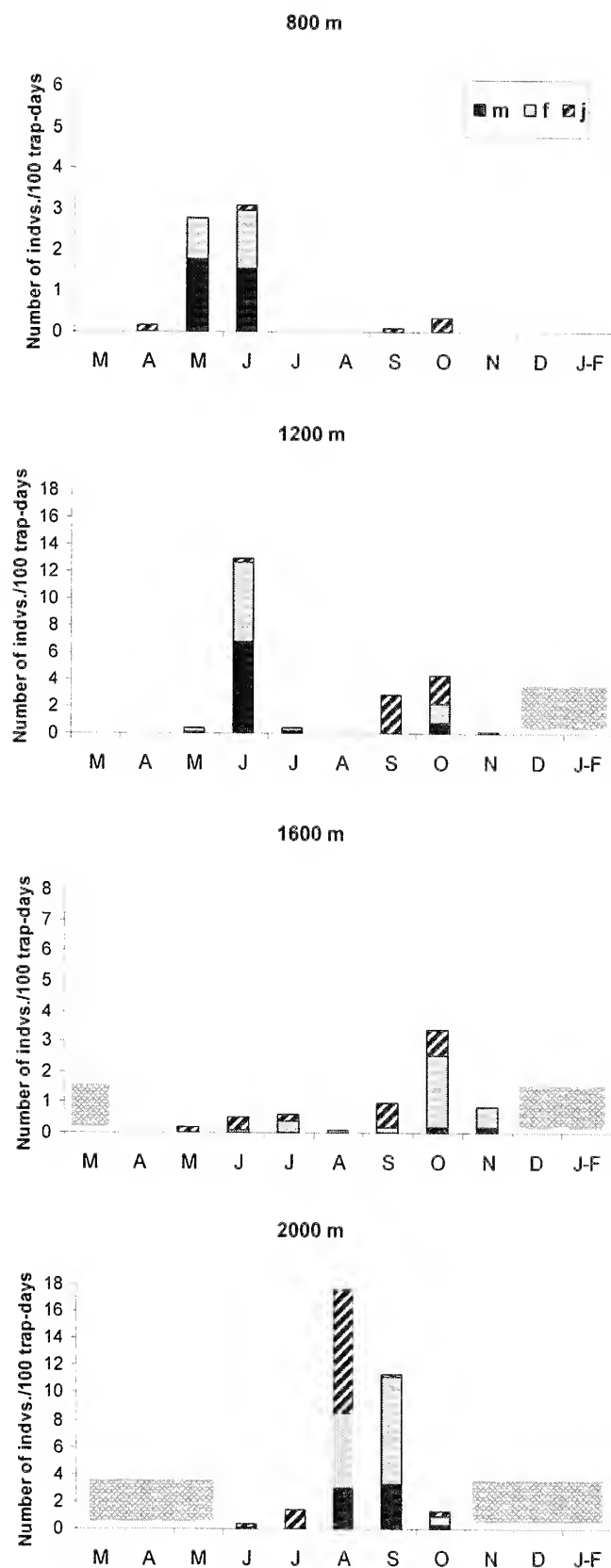


Figure 3.—Phenology of males (m), females (f) and juveniles (j) of *O. insulae* at different elevations. Grey horizontal bars indicate the months during which the sites were covered by snow.

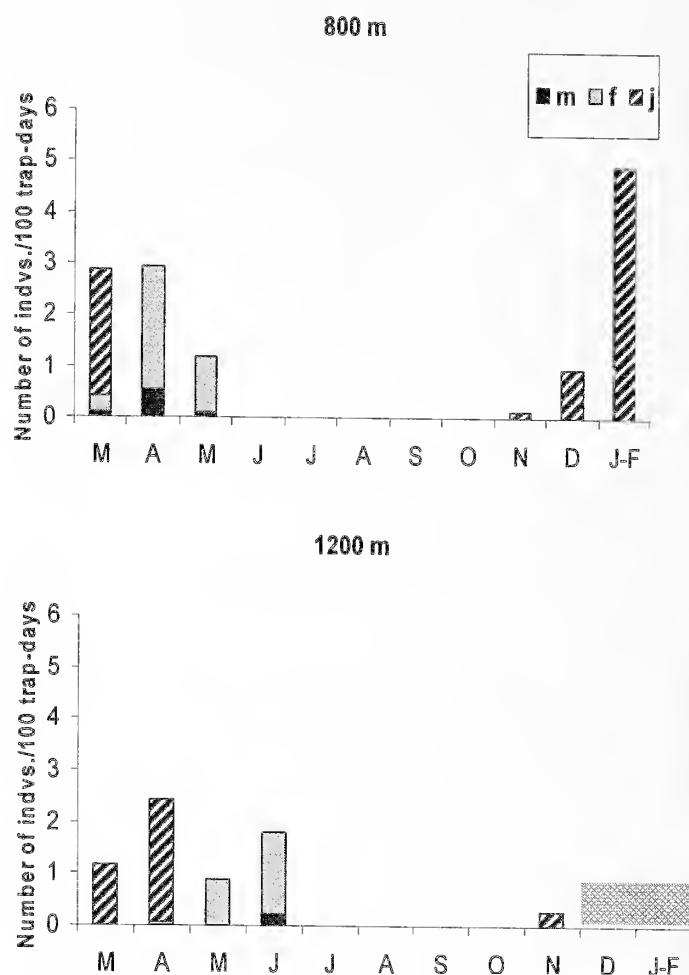


Figure 4.—Phenology of males (m), females (f) and juveniles (j) of *R. cretica* at different elevations. Grey horizontal bars indicate the months during which the sites were covered by snow.

and are ready to reproduce in September–October. Activity under the snow cannot be excluded, but is not demonstrated by the present data.

Opilio insulae presents a clearer phenological plasticity along the altitudinal gradient (Fig. 3). At the two lower elevations it presents a peak of activity in May–June, while at the two higher elevations it presents autumn peaks, in October at 1600 m and in August–September at 2000 m. At the first three elevations, juveniles present higher activity during September–October and at 2000 m during August.

Rafalskia cretica presents an early or mid spring peak of activity (Fig. 4), thus almost avoiding *O. insulae* and *L. insularis*. Very few immature individuals were found at the 1600 m site and none at 2000 m. At the two lower elevations the peaks of adult catches are shifted from April–May at 800 m to May–June at 1200 m, while immatures are active for a longer period at 800 m (December–March) than at 1200 m (March–April).

In a similar pattern, *G. cretaeum* presents a peak in March–April at 800/1200 m which is shifted towards April–May at 1600 m (Fig. 5). Interestingly at 2000 m there are two almost equal peaks of activity of all stages simultaneously present, one in June and another one in October. Although this might indicate a double generation per year or overlapping

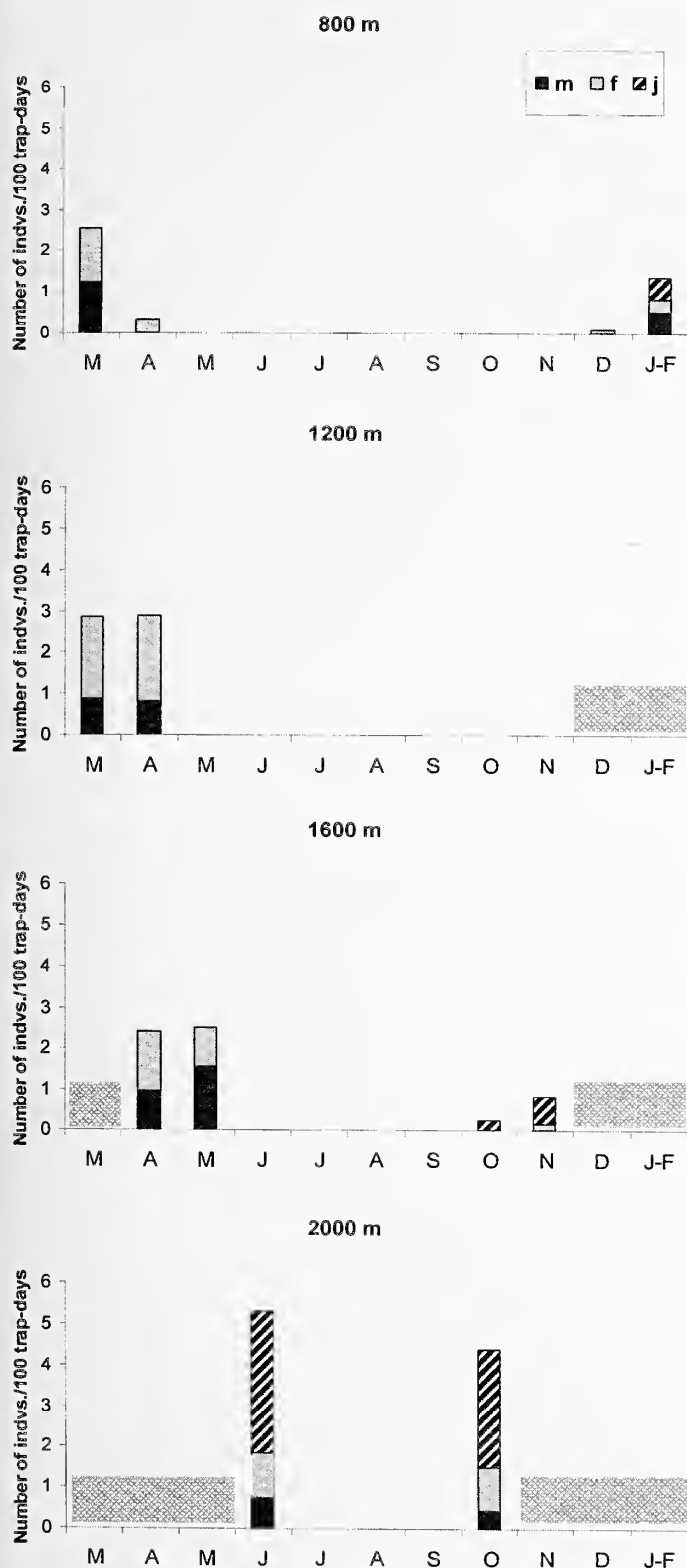


Figure 5.—Phenology of males (m), females (f) and juveniles (j) of *G. cretaeum* at different elevations. Grey horizontal bars indicate the months during which the sites were covered by snow.

generations, the number of individuals caught is too small to allow such an interpretation. Alternatively this double peak of activity might also correspond to the same single generation of harvestmen that become active only under the most favorable

conditions with optimum temperatures and humidity (i.e., June and October), while in the meantime (summer) they remain totally inactive due to their inability to tolerate the high aridity and high temperatures of this season.

Histicostoma creticum is restricted to the two lower elevations (800 and 1200 m), whereas *L. ghigii* to the two intermediate ones (1200 and 1600 m). Low numbers of both of them do not allow us any phenological interpretation. However, individuals of the former species were caught throughout the year (June, October, December and January at 800 m and April, July, November at 1200 m), while the latter species showed a tendency to be more active during autumn months (October–November).

At the two lower elevations, catches of all species cease for one (1200 m) or two (800 m) summer months (August and July–August, respectively). At the three higher elevations snow covered sampling traps for four (1200 m and 1600 m) and seven (2000 m) winter–spring months.

DISCUSSION

Phenology.—At Lefka Ori at all elevations harvestmen seem to have an annual life-cycle, as inferred from the phenological patterns (Figs. 2–5). The favorable period in which Opiliones at high elevations of Crete reach maturity is either in early autumn or in spring. Maturity lasts one to two months and is followed or preceded by a juvenile peak. In general, immature activity is expanded for a longer period within a year than mature stages, even at the highest elevations, where immature activity overlaps with that of adults (see for example *G. cretaeum* and *O. insulae* at 2000 m as extreme cases). This is common in species inhabiting high elevation habitats and signifies the shortening of biological processes within the year (Pinto-da-Rocha et al. 2007).

The phenological patterns of *L. insularis*, *R. cretica*, and *G. cretaeum* do not change along the altitudinal gradient, but their peaks of activity are shifted to one or two months later (*R. cretica* and *G. cretaeum*) or earlier (*L. insularis*) at the two higher elevations. It is important here to note that seasons are not the same at each elevation. Although lack of meteorological data allows us only to speculate, we suggest that with the rise of elevation, winter lasts longer and “squeezes out” spring and autumn. In this respect, at 2000 m October represents late autumn and June represents spring, whereas at 800 m, October and June are still very warm and dry months corresponding to “summer,” taking into account the high mean temperatures encountered in both periods. Hence Opiliones find similar climatic conditions in March–April at 800 and 1200 m and in May–June at 1600 and 2000 m (i.e., *G. cretaeum*) or in October–November at 800 m and in September at 2000 m (i.e., *L. insularis*).

The case of phenological differentiation of *O. insulae* (Fig. 3) is more pronounced, changing its peaks of activity from spring (800–1200 m) to late summer/autumn (1600–2000 m). The latter pattern is one of the very few cases of late summer activity peak among all taxa studied, at all elevations. The only species that presents the same pattern of activity at Lefka Ori is *Zelotes creticus* Kulczynski 1903, an endemic spider species that belongs to the family Gnaphosidae (Chatzaki et al. 2005b). This phenomenon may indicate that at the two higher elevations both mating and egg laying occur

in the same period; i.e., in late summer - beginning of autumn, while at the lower ones these processes are interrupted by the hot dry summer, during which animals remain inactive. Martens (1966) noted that the reproductive period of this harvestman in the seacoast region of Crete is from mid-April-June. This difference of phenological patterns between lowland and highland populations may possibly be justified by the climatic heterogeneity of the Cretan landscape. An alternative explanation however might be a taxonomic divergence of the species masked by morphological similarity, a phenomenon that has been observed in various taxa (e.g., Parmakelis et al. 2003 and references therein). This hypothesis remains to be further tested with molecular data.

A partitioning of the favorable periods, with peaks of activity following one another may be observed. As a result, activity periods of *R. cretica* and *G. cretaeum* never coincide with those of *O. insulae* and *L. insularis*. This seems to be the rule concerning arthropod phenology, since it has also been observed in spiders of the family Gnaphosidae (Chatzaki et al. 2005b) on Crete and in other Mediterranean regions (Urones et al. 1995) as well as in temperate ecosystems (Enders 1976; Toft 1976; Uetz 1977).

Cloudsley-Thompson (1962) places water conservation as the prime physiological problem for the survival of terrestrial invertebrates. Harvestmen are especially susceptible to water loss and this is a prime factor limiting species distributions (Hillyard & Sankey 1989; Pinto-da-Rocha et al. 2007). The fact that no harvestmen were caught for two months at 800 m and for one month at 1200 m, indicate a severe stress due to high aridity, which these animals try to overcome by ceasing their activity. Things are even more pronounced at the two higher elevations, the "High Desert" according to Rackham & Moody (1996). On one hand, snowfall and snow cover during four (1600 m) and seven months of the year, respectively, and on the other hand the extreme aridity of summer months (especially August at 2000 m), considerably restrict the suitable period for exploitation by harvestmen. A compromise between water conservation, limited time for activity, and avoidance of other species might result in the, still mysterious, mid-summer peak of activity of *O. insulae*.

Kinetic activity and species richness.—Janzen (1973), Janzen et al. (1976), Wolda (1987), and McCoy (1990) reported a decrease of the number of species and individuals of certain arthropod groups, mainly insects, along an altitudinal gradient. Almeida-Neto et al. (2006) showed a decline of both species richness and abundance of Opiliones in elevational gradients of three mountains in Brazil. Our data partially agree with the decrease in the number of species, but as far as kinetic activity of Opiliones is concerned a total increase in the number of individuals is observed, which is due to the impressive increase of three species, namely *L. insularis*, *O. insulae* and to a lesser extent *G. cretaeum*. Similarly, species of other taxa (i.e., members of the spider family Gnaphosidae (Chatzaki et al. 2005a), as well as some other families (Lycosidae, Dictynidae, Thomisidae, and Philodromidae (Chatzaki, unpublished data)) tend to reach extremely high numbers of individuals at the higher elevations of the same mountain system.

According to Hagvar et al. (1978) harvestmen is the largest group (as far as numbers of individuals are concerned) found

among other predatory arthropod communities at high elevations in Norway. The difference between our results and those found by Almeida-Neto et al. (2006) as far as the abundance along elevation is concerned, may lie in the fact that the range of climatic conditions that the tropical arthropods can tolerate cannot be as wide as that tolerated by animals of the temperate zone. Therefore, Opiliones of Crete should be able to reach higher elevations (hence harsher conditions) and create denser populations there. Another point which may partly explain this difference is the methodological bias caused by the fact that the authors measured the abundance of species as revealed by hand collecting and we measured the activity/abundance in the sense of pitfall catches.

In view of the identification of the origin of the mountain harvestmen of Crete, one has to follow the paleohistory of the island formation. The mountains of Crete have a very short history dating back to the beginning of the Pliocene (Meulenkamp et al. 1994) with an estimated elevation of 2000 m since then, which was accelerated mostly during the Pleistocene (Meulenkamp 1971). This newly and rapidly formed mountain landscape gave rise to new niches on the island. Taking into consideration that Crete was isolated from the mainland since the early Pliocene (Meulenkamp et al. 1988), the only available fauna to occupy the newly formed high elevations would be the already existing lowland species.

This is true for several taxa studied until now. Studies on ground beetles (Trichas 1996), terrestrial snails (Vardinoyannis 1994) and plants (Greuter 1972) agree that life of the Cretan mountains is mainly composed of derivatives of lowland endemics and a small number of old relicts. Chatzaki et al. (2005a) found one endemic but mostly non endemic high elevation specialists and lowland species which altogether compose the main part of the arachnofauna above 1600 m. Among the 20 species of Opiliones recorded on the entire island (Giltay 1932; Roewer 1927, 1940; Martens 1965, 1966; Gruber 1998), only six are reported above 800 m at Lefka Ori mountains. Three species increase in numbers of individuals along the altitudinal gradient and dominate at higher elevations (Table 1), two of which are Cretan endemics (*L. insularis* and *G. cretaeum*). At 2000 m, the latter are the only opilionid residents together with *O. insulae*. There are no high-elevation specialists, like in ground spiders, since all three of them are also found in the lowlands of Crete (for detailed references see Roewer 1927; Giltay 1932; Martens 1966).

In conclusion, harvestmen of the high elevations of Crete show a high tolerance to the extreme climatic conditions found in these environments and do not seem to be limited by them in order to create viable populations. The six species recorded above 800 m at Lefka Ori mountains represent the most physiologically tolerant species among the lowland residents of the island and none of them is a high-elevation specialist. Most species tend to exploit the favorable period of April-June and September-October. At the higher elevations, biological cycles are compressed to a narrow period in which climatic conditions allow the animals to be active.

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LITERATURE CITED

- Almeida-Neto, M., G. Machado, R. Pinto-da-Rocha & A.A. Giaretta. 2006. Harvestman (Arachnida: Opiliones) species distribution along three Neotropical elevational gradients: an alternative rescue effect to explain Rapoport's rule? *Journal of Biogeography* 33:361–375.
- Bonnefont, J.C. 1972. La Crête, étude morphologique. PhD thesis, Bibliothèque universitaire centrale, Université de Lille III, France. 845 pp.
- Chatzaki, M., P. Lymberakis, G. Markakis & M. Mylonas. 2005a. The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. *Journal of Biogeography* 32:813–831.
- Chatzaki, M., G. Markakis & M. Mylonas. 2005b. Phenological patterns of ground spiders (Araneae, Gnaphosidae) on Crete, Greece. *Ecologia Mediterranea* 31:33–53.
- Cloudsley-Thompson, J.L. 1962. Microclimates and the distribution of terrestrial arthropods. *Annual Review of Entomology* 7:199–222.
- De Lattin, G. 1949. Beiträge zur Zoogeographie des Mittelmeergebietes. *Verhandlungen der Deutschen Zoologischen Gesellschaft, Kiel* (1948). Leipzig, Supplementband 13:143–151.
- De Lattin, G. 1967. *Grundriss der Zoogeographie*. Gustave Fischer Verlag, Stuttgart und Jena. 602 pp.
- Di Castri, F. & V. Vitali-Di Castri. 1981. Soil fauna of Mediterranean climate regions. Pp. 445–478. *In* *Mediterranean Type Shrublands*. (F. Di Castri, D.W. Goodall & R.L. Specht, eds.). Elsevier, Amsterdam.
- Enders, F. 1976. Size, food finding and Dyar's constant. *Environmental Entomology* 5:1–10.
- Giltay, L. 1932. Aracnides recueillis par M. D'Orchymont au cours de ses voyages aux Balkans et en Asie Mineure en 1929, 1930 et 1931. *Bulletin du Museum Royal D' Histoire Naturelle de Belgique* 8(22):1–40.
- Greuter, W. 1972. The relict element of the Flora of Crete and its evolutionary significance. Pp. 161–177. *In* *Taxonomy, Phytogeography and Evolution*. (D.H. Valentine, ed.). Academic Press, London.
- Grove, A.T., J. Moody & O. Rackham. 1991. Crete and the South Aegean Islands: effects of changing climate on the environment. Unpublished report, Robinson College, University of Cambridge, Cambridge, UK. 445 pp.
- Gruber, J. 1998. Beitrag zur Systematik der Gattung *Dicranolasma* (Arachnida: Opiliones, Dieranolasmatidae). I. *Dicranolasma thracium* Starega und verwandte Formen aus Südosteuropa und Südwestasien. *Annalen des Naturhistorischen Museums in Wien* 100B:489–537.
- Hagvar, S., E. Ostbye & J. Melaen. 1978. Pit-fall catches of surface-active arthropods in some mountain habitats at Finse, south Norway. II. General results at group level, with emphasis on Opiliones, Araneida, and Coleoptera. *Norwegian Journal of Entomology* 25:195–205.
- Hillyard, P.D. & J.H.P. Sankey. 1989. Harvestmen: Keys and Notes for the Identification of the Species. *Synopses of the British Fauna*. Volume 4. Brill, Leiden, the Netherlands. 119 pp.
- Janzen, D.H. 1973. Sweep samples of tropical foliage insects: effects of season, vegetation types, elevation, time of day and insularity. *Ecology* 54:687–708.
- Janzen, D.H., M. Atarof, M. Farinas, S. Reyes, N. Rincon, A. Soler, P. Sorianp & M. Vera. 1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica* 8:193–203.
- Legakis, A. 1986. Comparative study of the soil arthropods of three ecosystems on Mount Hymettos (Attica Greece) *Biologia Gallo-Hellenica* 12:371–375.
- Lymberakis, P., M. Mylonas & S. Sfenthourakis. 2003. Altitudinal variation of oniscidean communities on Cretan mountains. *In* *The Biology of Terrestrial Isopods V*. (S. Sfenthourakis, P.B. Araujo, E. Hornung, H. Schmalfuss, S. Taiti & K. Szilávecz, eds.). *Crustaceana Monographs* 2:217–230.
- Mani, M.S. 1968. *Ecology and Biogeography of High Altitude Insects*. Dr. W. Junk. The Hague. 527 pp.
- Mani, M.S. 1990. *Fundamentals of High Altitude Biology*. Second edition. Oxford & IBH Publishing, New Delhi. 138 pp.
- Martens, J. 1965. Über südägäische Weberknechte der Inseln Karpathos, Rhodos und Kos. *Senckenbergiana Biologia* 46: 61–79.
- Martens, J. 1966. *Zoologische Aufsammlungen auf Kreta. III. Opiliones*. *Annales Die Naturhistorische Museum, Wien* 69:347–362.
- McCoy, E.D. 1990. The distribution of insects along elevational gradients. *Oikos* 58:313–322.
- Meulenkamp, J.E. 1971. The Neogene in the Southern Aegean area. *In* *Evolution in the Aegean*. (A. Strid, ed.) *Opera Botanica* 30: 5–12.
- Meulenkamp, J., M. Wortel, W. Van Wamel, W. Spakman & E. Hoogerduyn Strating. 1988. On the Hellenic subduction zone and the geodynamic evolution of Crete since the late Middle Miocene. *Tectonophysics* 146:203–215.
- Meulenkamp, J.E., G.J. van der Zwaan & W.A. van Wamel. 1994. On late Miocene to recent vertical motions in the Cretan segment of the Hellenic arc. *Tectonophysics* 234:53–72.
- Parmakelis, A., E. Spanos, G. Papagiannakis, C. Louis & M. Mylonas. 2003. Mitochondrial DNA phylogeny and morphological diversity in the genus *Mastus* (Beck, 1837): a study in a recent (Holocene) island group (Koufonisi, south-east Crete). *Biological Journal of the Linnean Society* 78:383–399.
- Pinto-da-Rocha, R., G. Machado & G. Giribet (eds.). 2007. *Harvestmen: the Biology of Opiliones*. Harvard University Press, Cambridge, Massachusetts. 516 pp.
- Rackham, O. & J. Moody. 1996. *The Making of the Cretan Landscape*. Manchester University Press, Manchester, UK. 273 pp.
- Roewer, C.-F. 1927. *Zoologische Streifzüge in Attika, Morea und besonders auf der Insel Kreta. I. Abhandlungen herausgegeben vom naturwissenschaftlichen Verein zu Bremen* 26:425–460.
- Roewer, C.-F. 1940. Neue Assamiidae und Trogludidae. Weitere Weberknechte X. Veröffentlichungen aus dem Deutschen Kolonial- und Übersee-Museum in Bremen 3:1–31.
- Sfenthourakis, S. 1992. Altitudinal effect on species richness of Oniscidea (Crustacea Isopoda) on three mountains in Greece. *Global Ecology and Biogeography* 2:157–164.
- Shanks, R.E. 1956. Altitudinal and microclimatic relationships of soil temperature under natural vegetation. *Ecology* 37:1–7.
- Stamou, G.P., S. Sgardelis & N.S. Margaris. 1984. Arthropods distribution pattern on a mountain gradient (Mt. Olympus, Greece). *Revue d'écologie et de biologie du sol* 21:491–505.
- Strid, A., M. Damanakis, E. Bergmeier & S. Matthas. 1995. Desertification in the White Mountains of Crete. A botanical study with special reference to the effects of grazing and wildfires. *Environment Research Program 1991–1994: Climatology and Natural Hazards*. Final report Contract EV5V-CT91-0031, European Community 78 pp.
- Toft, S. 1976. Life histories of spiders in a Danish beech wood. *Natura Jutlandica* 19:5–40.
- Trichas, A. 1996. Ecology and biogeography of ground Coleoptera in South Aegean (composition, temporal and biotopical variation

- and zoogeography of the families Carabidae and Tenebrionidae). PhD Thesis, University of Crete (in Greek), 395 pp.
- Uetz, G.W. 1977. Coexistence in a guild of wandering spiders. *Journal of Animal Ecology* 46:531–541.
- Urones, C., M. Jerardino & J.A. Barrientos. 1995. Datos fenologicos de Gnaphosidae (Araneae) capturados con trampas de caida en Salamanca (Espana). *Revue Arachnologique* 11:47–63.
- Vardinoyannis, K. 1994. Biogeography of land snails in the south Aegean island arc. PhD Thesis, University of Athens (in Greek), 330 pp.
- Wolda, H. 1987. Altitude, habitat and tropical insect diversity. *Biological Journal of the Linnean Society* 30:313–323.

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The chemical defenses of a stylocellid (Arachnida, Opiliones, Stylocellidae) from Sulawesi with comparisons to other Cyphophthalmi

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Abstract. Two female specimens of an undescribed species of stylocellid harvestman (Opiliones, Stylocellidae) from Sulawesi were extracted in methanol, and compounds in the product were identified by means of gas chromatography-mass spectrometry. Nineteen significant peaks were found, 12 of which were identified, indicating the presence of naphthoquinone, 2-tridecanone, 2-tetradecanone, 2-pentadecanone, 6-methyl-1,4-naphthoquinone, 6-methyl-1,4-naphthalenediol, and at least four unsaturated ketones. The spectrum differed both qualitatively and quantitatively from previously published data on *Siro exilis* Hoffman 1963 and *Cyphophthalmus duricorius* Joseph 1868 (Sironidae).

Keywords: *Siro*, *Cyphophthalmus*, exocrine products, ketones, naphthoquinones

Harvestmen (Opiliones) have a distinctive pair of prosomal exocrine glands opening to the surface via ozopores usually placed in the vicinity of the second leg pair. These glands produce a variety of substances (Table 1) effective in defense (e.g., Juberthie 1961a, 1961b, 1976; Eisner et al. 1971; Jones et al. 1977), and possibly with other functions as well. The secretions of approximately 48 species have been studied in detail up to this time. The results have been effectively reviewed by Gnaspini & Hara (2007; also see Hara et al. 2005), who presented a table listing the species and the compounds recorded from them. Forty-six compounds have been identified to date (numerous others are present but have not been identified), falling into the broad classes of long-chain alcohols and ketones, hydroxyquinones, phenols, and, more rarely, an alkaloid (nicotine), an amine (N,N-dimethyl-B-phenylethylamine), terpenoids (camphene, limonene) and bornyl esters (bornyl acetate and propionate) (Gnaspini & Hara 2007). A number of these compounds are unique or rare in nature, particularly in animals. Typically a single species produces a mixture of compounds, and the mixture of both identified and unidentified molecules may be characteristic of the particular taxon (family, genus, species) involved (Hara et al. 2005).

Although the defensive chemistry of Cyphophthalmi, Eupnoi and Laniatores has been studied for some species, that of many important higher taxa (i.e., Dyspnoi) remains completely uninvestigated. Our preliminary results (unpublished data) suggest that travunioids, only a single species of which has been examined so far, are extraordinarily diverse in their chemistry. Studies of Grassatores have concentrated on just a few families (Cosmetidae, Gonyleptidae, Manaosbiidae, Stygnommatidae) in this very diverse assemblage.

Defensive chemistry of the basal and divergent harvestman suborder Cyphophthalmi (e.g., see Giribet et al. 2002 for the phylogenetic placement of Cyphophthalmi) is interesting because if the composition of defensive secretions is of any phylogenetic use, its ancestral state in this group could be used to polarize the characters higher in the tree and to optimize the ancestral state of the defensive substances in Opiliones. But to date, only two cyphophthalmid species, *Siro exilis* Hoffman

1963 of North America, and *Cyphophthalmus duricorius* Joseph 1868 of Europe, have been studied for their defensive secretions (Raspotnig et al. 2005). Both of these species belong to the same family, Sironidae, while members of the other extant five families remain unexamined. The secretions of the two sironids consist of complex arrays of ketones and naphthoquinones.

In this paper, we present data on the secretion of an undescribed species probably belonging to the genus *Stylocellus*, family Stylocellidae. This species will be named and described in a forthcoming revision of the family by Ronald Clouse. In the current phylogenies of cyphophthalmids, the families Stylocellidae or Pettalidae appear basal within the suborder (Giribet & Boyer 2002; Boyer et al. 2007), although their stable placement is still debatable. The family Stylocellidae is found exclusively in Southeast Asia, from Southern China and Northeast India to the western side of New Guinea, in the Indonesian province of Irian Jaya, and the Philippine island of Palawan (Shear 1993; Clouse & Giribet 2007; Giribet et al. 2007; R. Clouse, in progress). The species we studied was collected on the Indonesian island of Sulawesi and is tentatively assigned to the genus *Stylocellus*, although the whole generic systematics of the family is currently under re-examination (R. Clouse & G. Giribet, in progress).

METHODS

Two female *Stylocellus* specimens of a yet undescribed species (Fig. 1) were collected alive in Bantimurung, Sulawesi (5°02'33"S, 119°44'08"E; 348 m elev.; Giribet locality number 512; collected 28 June 2008, R. Clouse, G. Giribet, C. Rahmadi, leg.; MCZ DNA101938), shipped alive to WAS, and extracted in about 0.5 ml of USP methanol. The extracts of the two specimens were pooled. The code number 06-172 was assigned to the specimens, both of which will be placed as vouchers in the Museum of Comparative Zoology, Cambridge, Massachusetts. The analysis of the extract was performed by THJ. Gas chromatography-mass spectrometry was carried out in the EI mode using a Shimadzu QP-5000 GC/MS equipped with an RTX-5, 30 m × 0.25-mm i.d. column. The instrument was programmed from 60° C to 250° C at 10°/min. Identification of components was accomplished

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Table 1.—Distribution of defensive secretions in Opiliones. For more detail, see Gnaspini & Hara (2007).

Taxon	Compounds
Suborder Cyphophthalmi	Ketones, naphthoquinones
Suborder Eupnoi	
Family Phalangidae	naphthoquinones
Family Sclerosomatidae	ketones, alcohols
Suborder Dyspnoi	unknown
Suborder Laniatores	
Infraorder Insidiatores	Amines, bornyl esters, terpenes, alkaloids
	Phenols, methylquinones
Infraorder Grassatores	Benzoquinones, phenols



Figure 1.—One of the extracted specimens of stylocellid from Bantimurung, Sulawesi, photographed alive by G. Giribet. Specimen is about 6.5 mm in body length.

using NIST/EPA/NIH mass spectral library on CD-rom, version 1.7 (1999) and the NIST/EPA/NIH mass spectral library version 2.0d (2005).

RESULTS AND DISCUSSION

After gas chromatography-mass spectrometry examination, 19 significant peaks were identified in the extract. The major peaks in our analysis indicate the presence of naphthoquinone, 2-tridecanone, 2-tetradecanone, 2-pentadecanone, 6-methyl-1,4-naphthoquinone, 6-methyl-1,4-naphthalenediol, and at

least four unsaturated ketones, two of which correspond to peaks S and U as noted by Raspotnig et al. (2005), so we have adopted their identification of these compounds (Table 2).

Table 3 compares the analyses of the three species of Cyphophthalmi. Chloronaphthoquinones are unique in the two sironid species (and as exocrine products of arthropods [Raspotnig et al. 2005]), but were not found in the stylocellid species; likewise undecan-2-one, 6-tridecen-2-one and 7-tridecen-2-one were absent from the secretion of *Stylocellus*. It is possible that these unusual compounds came from the males included in the sironid samples. Furthermore, the stylocellid secretion contained 6-methyl-1,4-naphthalenediol, a reduction product of 6-methyl-1,4-naphthoquinone, which did not occur in the two sironids. The percent composition of compounds that were common to the three species shows strong differences between the stylocellid and the two sironids, and to a lesser degree, between *Siro exilis* and *Cyphophthalmus duricorius*. While 2-tridecanone made up about 20% of the secretion of both sironids, it comprised 50% in the stylocellid; 1,4-naphthoquinone and 6-methyl-1,4-naphthoquinone were found in very small amounts in the stylocellid, but at values from about 12% to nearly 18% in the sironids; pentadecan-2-one was at 13.8% for the stylocellid, but less than 1.7% for the sironids, and so on.

In summary, we may observe that while the composition of the secretions of the three species is similar in constituting mixtures of ketones and naphthoquinones, there are significant differences both qualitative and quantitative. Some of the differences could be due to the fact that we extracted our animals in methanol, while Raspotnig et al. (2005) used hexane. Raspotnig et al. (2005) found that the composition of the secretions in the two species studied by them was highly consistent from individual to individual within species, as has been reported in numerous previous studies of harvestman defensive secretions. This lessens our concern about the small size of our sample versus the much larger samples taken by Raspotnig et al. (2005); the remote location and relative rarity of the animals we studied makes it unlikely that large samples will be available in the near future.

The secretion of the stylocellid seems to contain fewer compounds than found by Raspotnig et al. (2005), who identified at least tentatively all of the 24 peaks they found (as opposed to our 19). However, very small peaks were not considered by us. Nevertheless, the observation about the

Table 2.—Compounds and percent composition identified in methanol extract of whole females of the stylocellid from Sulawesi. See also Fig. 2.

Peak	Compound	Relative %	Peak code in Raspotnig, et al. 2005
1	1,4-Naphthoquinone	2	E
2	2-Tridecanone	42	J
3	6-methylnaphthoquinone	1	L
4	Methyl branched 2-tridecanone	8	M or N
5	2-Tetradecanone	9	M or N
6	6-Methyl-1,4-naphthalenediol	1	Not detected
7	2-Pentadecadienone	8	S
8	2-Pentadecenone	7	U
9	Unsaturated ketone a	3	?
10	Unsaturated ketone b	3	?
11	2-Pentadecanone	14	W
12	2-Methoxy-1,4-naphthoquinone	3	Not detected

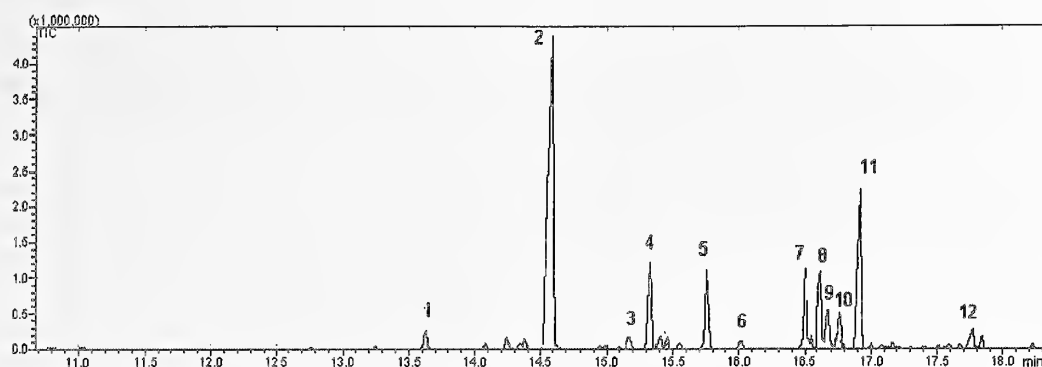


Figure 2.—Gas chromatographic profiles of whole-body methanol extract of stylocellid from Sulawesi. Identified peaks are numbered; numbers correspond to those in Table 2.

number of compounds would hold on the basis of the number of peaks alone. Aside from 5-methylnaphthoquinone, not found in the sironids, the stylocellid secretion is strongly dominated by ketones and lacks the diversity of naphthoquinones found in sironids. If stylocellids are in fact a sister group to other Cyphophthalmi, this observation suggests that the other naphthoquinones, especially the chlorinated ones, have been added in the course of evolution (or lost in the stylocellid lineage), and perhaps that ketones dominated the secretion of the common ancestor of extant Opiliones. Quinones may have been co-opted later from substances used by all arthropods to sclerotize cuticular proteins. However, proper polarization of this character requires first, a well-resolved cyphophthalmid phylogeny and second, a proper outgroup comparison. Since Opiliones' putative outgroups (Solifugae, Scorpiones, and Pseudoscorpiones; e.g., Wheeler & Hayashi 1998; Giribet et al. 2002; Shultz 2007) do not have this type of secretion, polarization may be difficult.

Rasputnig et al. (2005) pointed out that while both ketones and naphthoquinones are found in Cyphophthalmi, sclerosomatids (suborder Eupnoi) secrete only ketones (and alcohols) and the single phalangiid studied (also an Eupnoi), naphthoquinones. In Laniatores, Grassatores utilize phenols and

methylquinones, while the single member of Insidiatores analyzed uses an eclectic mix of N,N-dimethyl-B-phenylethylamine, nicotine, bornyl esters, and terpenes. But again we must point out the strong bias in the data. Most of the species studied have been either Grassatores or sclerosomatids (see Table 1), while Dyspnoi and the Eupnoi family Caddidae, two groups of significant phylogenetic importance, have not been studied chemically at all.

In addition, no study has yet been made of the effect of collection method on the results of the analysis of harvestman secretions. In our studies, we are using methanol to extract whole bodies of live specimens, but other solvents, such as hexane, have been used in other laboratories. In some studies, live animals are induced to secrete their defensive compounds, which are collected either by micropipettes, fine glass tubing, or by absorption on filter paper. Thus we do not know if differences between species where different collection methods were used are real, or artifacts of the different methods. Certainly the fact that in many species the secretion of the repugnatorial glands is mixed with regurgitate from the gut could play a role if the already-mixed secretion is collected. The question of sample size also arises; here we used pooled extract from only two animals of the same sex, while

Table 3.—Comparison of percent composition of secretions of the stylocellid from Sulawesi with those of *Siro exilis* and *Cyphophthalmus duricorius* (data from Rasputnig et al. 2005). Confidence limits are given for the data on *S. exilis* and *C. duricorius* because Rasputnig et al. (2005) were reporting on individual extractions from 26 and 95 adult specimens respectively (for a complete list of compounds identified from the sironid species, see Rasputnig et al. [2005]). Our measurements are single points representing a pooled extraction of two adults due to the smaller collections of stylocellids when compared to the two sironid species studied previously. Bold figures represent the largest amount if significant differences are present; if two figures in a row are in bold type, there was no statistically significant difference between those two.

Compound	Stylocellid	<i>S. exilis</i>	<i>C. duricorius</i>
2-Tridecanone	50.0	20.28±3.79	20.21±3.56
7-Tridecen-2-one	not identified	15.47±1.35	18.98±2.38
1,4-Naphthoquinone	1.7	14.01±1.9	17.61±2.82
6-Methyl-1,4-naphthoquinone	1.0	13.08±1.43	12.15±2.03
Undecan-2-one	not identified	0.57±0.19	9.71±1.59
4-Chloro-1,2-naphthoquinone	not identified	11.83±1.68	7.09±2.44
6-Tridecen-2-one	not identified	4.13±0.92	4.02±1.03
Pentadecan-2-one	13.8	1.68±0.5	0.01±0.02
6-Methyl-4-chloro-1,2-naphthoquinone	not identified	4.30±1.24	0.36±0.51
2-Tetradecanone	8.0	1.10±0.33	0.65±0.25
Pentadecadecione	8.0	3.0±0.86	0.04±0.06
Pentadecenone	6.7	4.5±1.14	0.03±0.05
6-Methyl-1,4-naphthalenediol	0.7	not identified	not identified

Rasputnig et al (2005) used large samples including both sexes and juveniles, and analyzed each extract individually. Previous studies of harvestman defensive secretions vary greatly as to the numbers of individuals sampled, and in some cases numerous animals were used, but the samples were pooled for analysis. In the near future we hope to carry out a study using different collection methods and solvents on numerous individuals of the same species, in order to compare the effects of these methods.

Hara et al. (2005) were able to map the composition of the secretions of 22 gonyleptids (Laniatores, Grassatores) on a phylogenetic tree constructed from other characters. They found rampant homoplasy, but noted that closely related compounds (pairs of phenols and quinones) could easily be transformed into one another by oxidation or reduction, suggesting that "families" of such compounds could represent synapomorphies as transformation series of compound families. However, their final conclusions were ambiguous. On the one hand, it appeared that the great diversity of the secretions did not allow the recognition of phylogenetic lineages, with some exceptions, but on the other, they hoped that the analysis of more species and the addition of metabolic sequences and interchangeable compounds might provide phylogenetic information in the future. We agree with this position and plan to continue to analyze opilionid defensive secretions not only in a search for molecules new to science or new to arthropods, but also with the expectation that more data will help to clarify phylogenetic relationships within Opiliones.

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LITERATURE CITED

- Boyer, S.L., R.M. Clouse, L.R. Benavides, P.J. Schwendinger, I. Kuranarathna & G. Giribet. 2007. Biogeography of the world: a case study from cyphophthalmid Opiliones, a globally distributed group of arachnids. *Journal of Biogeography* 34:2070–2085.
- Clouse, R.M. & G. Giribet. 2007. Across Lydekker's Line — first report of mite harvestmen (Opiliones : Cyphophthalmi : Stylocellidae) from New Guinea. *Invertebrate Systematics* 21:207–227.
- Eisner, T., A.F. Kluge, J.E. Carrel & J. Meinwald. 1971. Defense of phalangid: liquid repellent administered by leg dabbing. *Science* 173:650–652.
- Giribet, G. & S.L. Boyer. 2002. A cladistic analysis of the cyphophthalmid genera (Opiliones, Cyphophthalmi). *Journal of Arachnology* 30:110–128.
- Giribet, G., G.D. Edgecombe, W.C. Wheeler & C. Babbitt. 2002. Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data. *Cladistics* 18:5–70.
- Giribet, G., P.P. Sharma & D.B. Bastawade. 2007. A new genus and species of Cyphophthalmi (Arachnida: Opiliones) from the north-eastern states of India. *Zoological Journal of the Linnean Society* 151:663–670.
- Gnaspini, P. & M.R. Hara. 2007. Defense mechanisms. Pp. 374–399. *In* Harvestmen: The Biology of Opiliones. (R. Pinto-Da-Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, MA.
- Hara, M.R., A.J. Cavaleiro, P. Gnaspini & D.Y.A.C. Santos. 2005. A comparative analysis of the chemical nature of defensive secretions of Gonyleptidae (Arachnida: Opiliones: Laniatores). *Biochemical Systematics and Ecology* 33:1210–1225.
- Jones, T.H., J. Meinwald, K. Hicks & T. Eisner. 1977. Characterization and synthesis of volatile compounds from the defensive secretions of some "daddy longlegs" (Arachnida: Opiliones: *Leiobunum* spp.). *Proceedings of the National Academy of Sciences USA* 74:419–422.
- Juberthie, C. 1961a. Structure des glandes odorantes et modalités d'utilisation de leur sécrétion chez deux Opilions Cyphophthalmes. *Bulletin de la Société zoologique de France* 86:106–116.
- Juberthie, C. 1961b. Structure et fonction des glandes odorantes chez quelques Opilions (Arachnida). *Verhandlungen der Deutschen Zoologischen Gesellschaft in Saarbrücken* 1961:533–537.
- Juberthie, C. 1976. Chemical defence in soil Opiliones. *Revue d'Écologie et de Biologie du Sol* 13:155–160.
- Rasputnig, G., G. Fauler, M. Leis & H.J. Leis. 2005. Chemical profiles of scent gland secretions in the cyphophthalmid opilionid harvestmen, *Siro duricorius* and *S. exilis*. *Journal of Chemical Ecology* 31:1353–1368.
- Shear, W.A. 1993. New species in the opilionid genus *Stylocellus* from Malaysia, Indonesia and the Philippines (Opiliones, Cyphophthalmi, Stylocellidae). *Bulletin of the British Arachnological Society* 9:174–188.
- Shultz, J.W. 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. *Zoological Journal of the Linnean Society* 150:221–265.
- Wheeler, W.C. & C.Y. Hayashi. 1998. The phylogeny of extant chelicerate orders. *Cladistics* 14:173–192.

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Natural history of coastal Peruvian solifuges with a redescription of *Chinchippus peruvianus* and an additional new species (Arachnida, Solifugae, Ammotrechidae)

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Abstract. Two species of *Chinchippus* (Ammotrechidae) were studied in central Peru. Both species are endemic to the hyper-arid coastal desert and appear to derive most of their energy and nutrients from maritime prey, such as intertidal amphipods feeding on beach-cast algae or as arthropod scavengers feeding upon seabird and pinniped carcasses. Data on the spatial distribution of the two species were obtained from analyzing stomach contents of one common predator, the gecko *Phyllodactylus angustidigitus*, and suggest that both species are more abundant in insular than in mainland habitats. We redescribe *Chinchippus peruvianus* Chamberlin 1920, known only from a female specimen and describe the male for the first time while *C. viejaensis* is recognized as new. The new species is distinguished from *C. peruvianus* by its darker coloration, smaller size, and differences in cheliceral dentition.

Keywords: Camel spiders, coastal desert, ecology, Gekkonidae, Peru, *Phyllodactylus angustidigitus*, taxonomy

In the process of investigating the ecology of terrestrial organisms in the coastal desert and guano islands of central Peru, we have come across a series of *Chinchippus peruvianus* Chamberlin 1920 and a closely related species. These solifuges, along with other terrestrial predators, thrive in places that could be defined as a barren land of gravel, sand, and granitic outcrops – a moonscape where arachnids and lizards somehow manage to survive, reproduce, and colonize new habitats. The western coast of South America is among the driest places on Earth (Dietrich & Perron 2006), where arid conditions have persisted for the last 14 million years (Alpers & Brimhall 1988). Facing this hyper-arid ecosystem is one of the world's most productive marine ecosystems, the Peru-Chile cold current (Tarazona & Arntz 2001). The stark contrast in productivity promotes the exchange of energy and nutrients between these two adjacent ecosystems, and marine-derived resources subsidize terrestrial predators along the Peruvian coast (Catenazzi & Donnelly 2007a) and in other coastal deserts (Polis & Hurd 1996). In this study we describe the taxonomy and natural history of the two *Chinchippus* species and explore their distribution in relation to the availability of marine-derived resources.

The genus *Chinchippus* was established by Chamberlin (1920) based on a single female from the Peruvian island of Chincha. He considered it to belong to the African family Daesiidae. Roewer (1934) included *Chinchippus* in the ammotrechid subfamily Saronominae based on the segmentation of legs I, II, and IV and the palpal spination. Muma (1976) tentatively included it with the saronomines although its placement was still based on Chamberlin's sole female. Based on Chamberlin's single female, the genus *Chinchippus* can be recognized by: all the legs having a single tarsal segment, no claws on leg I, stridulating ridges on the mesal

surface of the chelicera, lateral plates of the "rostrum" shorter than the median plates, and a recurved cephalothorax.

METHODS

One of us (AC) conducted fieldwork at the Paracas National Reserve (PNR; 13°51'S, 76°16'W), ~19 km S of the Chinchas islands, in the Peruvian Region of Ica (Fig. 1). This reserve protects 335,000 ha of coastal waters and subtropical Peruvian coastal desert, including a variety of arid and hyper-arid terrestrial habitats. The PNR includes the Paracas Peninsula, which forms the southern edge of Paracas Bay, and the islands of Sangayán and La Vieja. The coastal topography is extremely heterogeneous and includes sandy, gravel, pebble and boulder beaches; cliffs; wind-shaped landforms; and uplifted ancient beaches. The climate is characteristic of the arid coastal desert of Peru and northern Chile and receives less than 2 mm of rain per year (Craig & Psuty 1968). Temperatures are mild and range between an average high of 22.9° C in February to an average low of 16.3° C in August (Environmental Resources Management 2002).

Using the methods of Muma (1951), Brookhart & Muma (1981, 1987), Muma & Brookhart (1988), and Brookhart & Cushing (2004), we measured total length; length of palpus, leg I, leg IV; length and width of chelicera and propeltidium; width of base of fixed finger; and length and width of female genital operculum using Spot Basic™ with an Olympus SZX12 microscope at 25× magnification. All measurements are in millimeters. Ratios used previously by Brookhart & Cushing (2002, 2004) were computed. These ratios are as follows: A/CP: the sum of the lengths of palpus, leg I, and leg IV divided by the sum of length of chelicera and propeltidium indicating length of appendages in relation to body size. Long-legged species have larger A/CP ratios. Because there is no fonal notch, the cheliceral width/fixed finger width ratio is used to indicate whether the fixed cheliceral finger of the male is thin or robust in relation to the size of the chelicera. Genital operculum length/genital operculum width represents the

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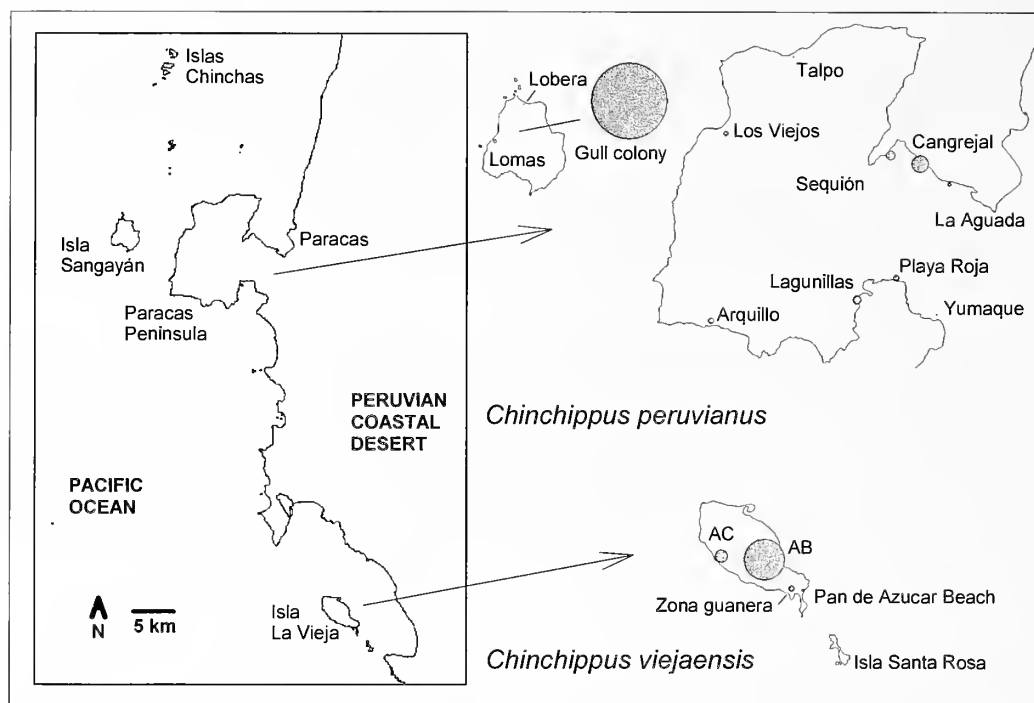


Figure 1.—Map of study localities and spatial variation in the frequency of occurrence of *Chinchippus peruvianus* and *C. viejaensis* in stomach contents of the gecko *Phyllodactylus angustidigitus* at Isla Sangayán (3 sites), the Paracas Peninsula (10 sites) and Isla La Vieja (4 sites), central Peru. The diameter of circles represents frequency of occurrence ranging from 0% (Yumaque, Paracas Peninsula) to 100% (gull colony, Isla Sangayán).

relative size of the female genital operculum in terms of length and width. Species determinations were based on a combination of color comparisons, the shape and dentition patterns of the male chelicerae, palpal setation, and color patterns of the propeltidium, palpus, and legs. The shape of the female chelicerae and the female genital operculum margin were observed using the method of Brookhart & Cushing (2004). Cheliceral dentition patterns were based on the method of Maury (1982) in which, for example, PT-1-2-AT indicates one primary tooth, two intermediate teeth, and one anterior tooth.

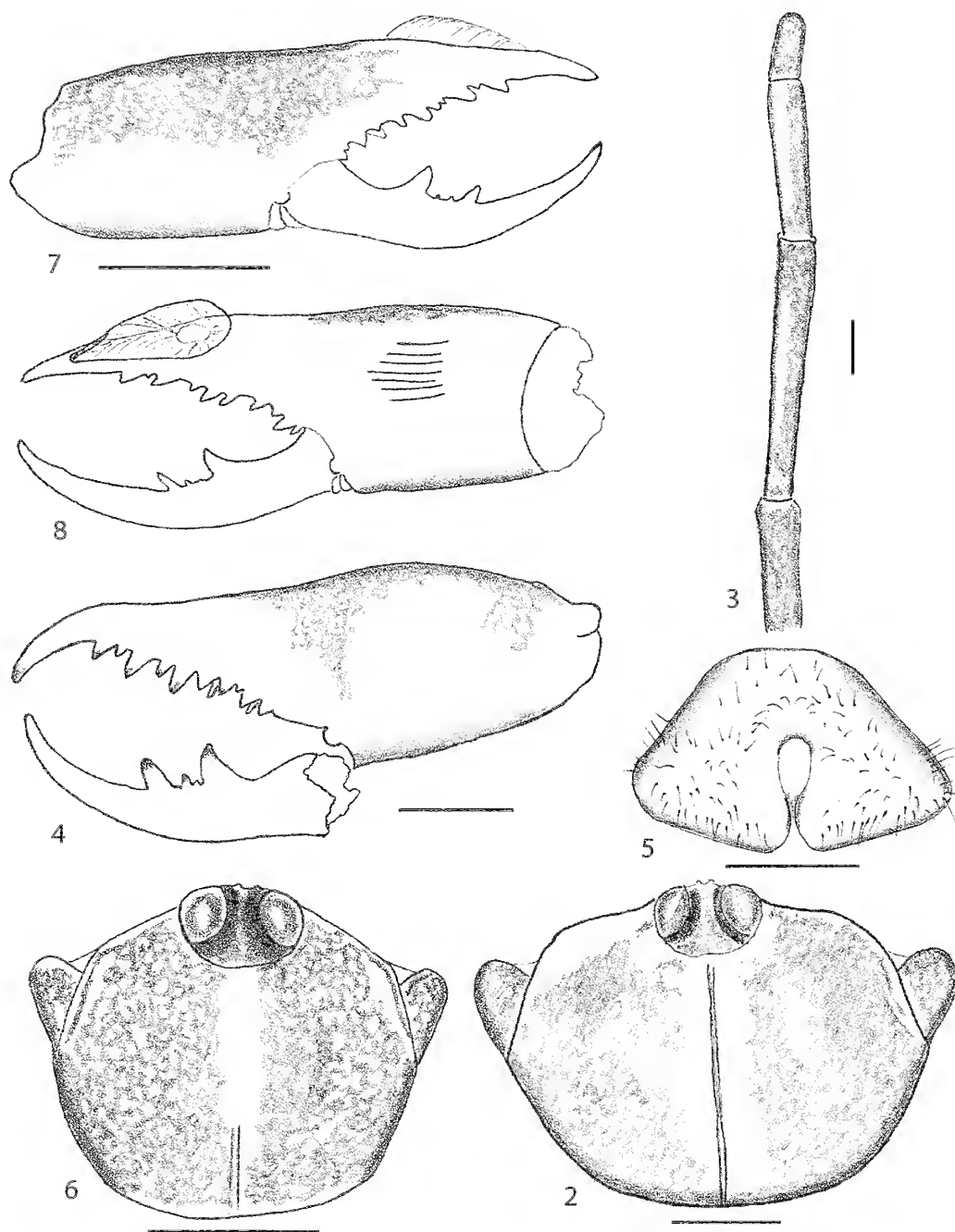
Collections from which material was borrowed or deposited include the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts, USA (MCZ); the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM); and the Denver Museum of Nature and Science, Denver, Colorado, USA (DMNS).

We collected solifuges by using pitfall traps or by opportunistically collecting during nocturnal walks. We used pitfall traps consisting of plastic cups 9 cm in diameter and 10 cm deep filled with a mix of water and detergent along the southern end of Paracas Bay between 6–9 January and 6–11 April 2003. During the January trapping, a series of three pitfall traps were placed near sandy/muddy beaches in coastal dunes and the adjacent desert at 5, 10, and 15 m distance from shore. During the April trapping, we placed pitfall traps near shelly beaches along transects at 0, 0.1, 1, 10 and 100 m from shore. We installed three transects, each one composed of three lines of pitfall traps. In addition to pitfall trapping, we also counted and measured solifuges in 90 1-m² plots in the

intertidal zone in March 2003. Count data of the March and April trapping period were reported by Catenazzi & Donnelly (2007a). Here we report count data from the January trapping, as well as solifuge size-distribution data from the March trapping along the shelly beach. Means are reported \pm SE and statistical tests are considered significant at $P < 0.05$.

We include anecdotal observations on predators, prey, and behavior of solifuges observed in the field. Some of these observations were captured in photographs and video and are available online at <http://acatenazzi.googlepages.com/chinchippus>.

We relied upon stomach content examinations of the gecko *Phyllodactylus angustidigitus* Dixon & Huey 1970, a common and ubiquitous reptile in the coastal desert, to better understand the distribution of solifuges in the coastal desert of the Paracas Peninsula and the islands of Sangayán and La Vieja. These geckos feed opportunistically on any live terrestrial arthropod of appropriate size, including beach hoppers, centipedes, arachnids, and insects (Catenazzi & Donnelly 2007a), and do not masticate their prey, facilitating the task of identifying prey remains in the stomachs. Stomach contents were obtained by inserting a small catheter through the esophagus and by flushing the geckos' stomachs with water (Catenazzi & Donnelly 2007a). Stomach contents ($n = 814$) were collected from Isla La Vieja (4 sites), Isla Sangayán (3 sites), and the Paracas Peninsula (10 sites). We considered whole prey items only to calculate frequency of occurrence of *Chinchippus* prey with respect to number of geckos sampled and with respect to total number of prey items in all pooled stomach contents.



Figures 2–8.—*Chinchippus peruvianus*. 2–5. Female holotype, Peru: Ica: Islas Chinchas, 26 October 1919, R. C. Murphy (MCZ 519): 2. Propeltidium, dorsal; 3. Palp, dorsal; 4. Right chelicera, ectal; 5. Genital operculum, ventral. 6–8. Male, Peru, Cangrejal, 25 March 2003, A. Catenazzi: 6. Propeltidium, dorsal; 7. Right chelicera, ectal; 8. Right chelicera, mesal. Scale bars = 1 mm.

TAXONOMY

Family Ammotrechidae Roewer 1934
 Subfamily Saronominae Roewer 1934
 Genus *Chinchippus* Chamberlin 1920
Chinchippus peruvianus Chamberlin 1920
 (Figs. 2–8)

Chinchippus peruvianus Chamberlin 1920:36–37.

Material examined.—*Type*: PERU: Ica Region: female holotype, Islas Chinchas (13°37'37"S, 76°23'21"W), 26 October 1919, R.C. Murphy (MCZ 519).

Other material: PERU: Ica: Paracas Bay: 2 ♀ (1 from the stomach content of *Phyllodactylus angustidigitus*), Cangrejal (13°51'03"S, 76°17'08"W, 1 m elev.), 3 March 2003, A. Catenazzi (DMNS); 2 ♂ same data except 25 March 2003, A. Catenazzi (DMNS); 2 ♀, La Aguada (13°51'44"S, 76°16'15"W, 2 m elev.), 7 January 2003, A. Catenazzi (DMNS); 1 ♂, Museo de Paracas Julio C. Tello (13°52'00"S, 76°16'26"W, 13 m elev.), 25 March 2003, A. Catenazzi (DMNS).

Diagnosis.—*Chinchippus peruvianus* is larger and lighter than *C. viejaensis* and differs by cheliceral dentition (compare Figs. 7 and 11).

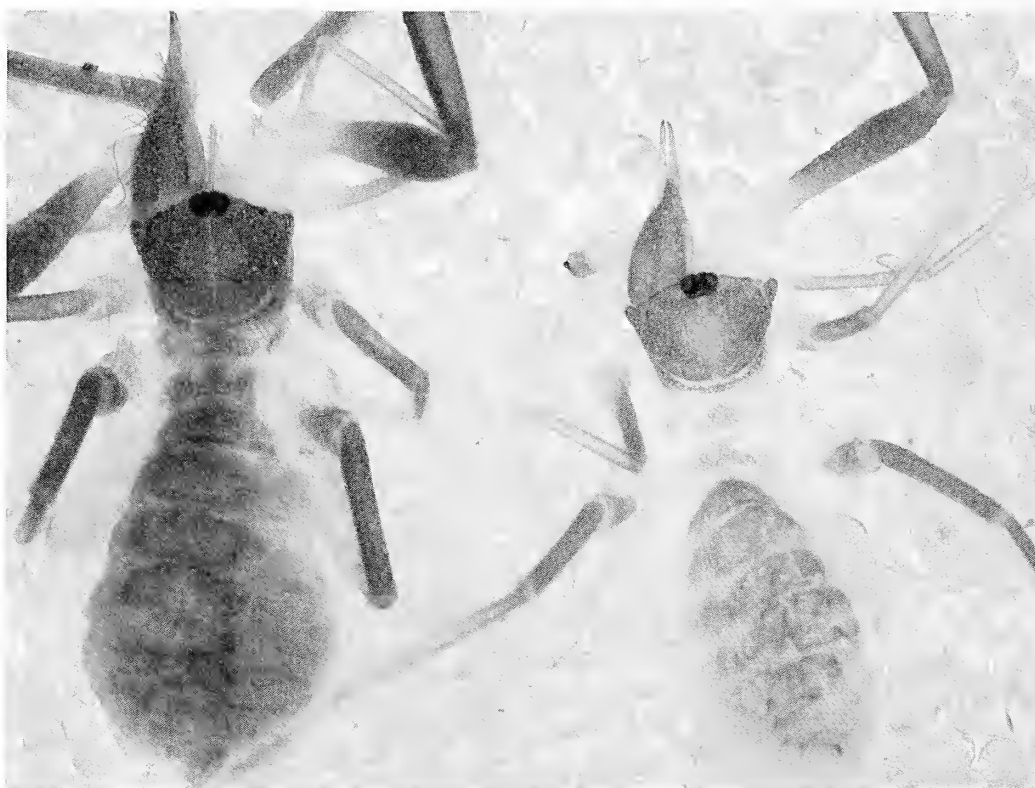


Figure 9.—Habitus of *Chinchippus viejaensis*. Male (left), female (right).

Description.—*Female holotype*: Color: Overall color as described by Chamberlin (1920): chelicera mottled violet-brown; propeltidium violet-brown with a pale creamy light ovate area highlighted by a lighter median band extending from eye tubercle to posterior end of propeltidium; eye tubercle dark (Fig. 2); mesapeltidium, metapeltidium white; abdomen creamy yellow with a median mottled violet-brown stripe dorsally and creamy grey laterally and dorsally; palp darker on tarsus and femur, metatarsus and tibia pale to white, coxa creamy yellow (Fig. 3). Legs II, III, IV light, violet-brown on tarsus, metatarsus, and apical parts of the tibia, darker on distal end of tibia as in femur, coxa creamy white. Leg I creamy white except for femur, which is a light violet; malleoli white.

Chelicera: fondal teeth graded III, I, IV, II; Fixed finger teeth arranged 1-PT-1-MT-1-AT; movable finger teeth arranged PT-1-2-AT (Fig. 4; however, Chamberlin illustrates PT-1-AT). Six to seven stridulatory ridges on the meso dorsal aspect of the chelicerae.

Palp: tarsus/metatarsus ratio 3:1.

Legs: leg IV tarsus with ventral paired setae arranged 2-2-2-2-1.

Abdomen: genital operculum: clavate with anterior arms thick, median edge recurved forming a deep central cavity accessing the genital opening, posterior edge straight (Fig. 5).

Male: Color: color pattern, including appendages, the same as in the female except the median pale stripe extends only from the posterior third of the propeltidium towards the ocular tubercle (Fig. 6); chelicera mottled dorsally and ectally coalescing anteriorly (Fig. 7); pale ventrally; malleoli white.

Chelicera: fondal teeth graded I-III-II-IV ectally and I, III, II mesally; fixed finger teeth arranged PT-1-2-MT-1-AT;

movable finger teeth arranged PT-1-2-AT (Figs. 7, 8). Flagellum a broadly elliptical structure attached to the fixed finger above the primary tooth, slightly to the dorsal edge. The attachment appears to be a concave structure. No setae or fringes are seen on the edges of the flagella. It bears some resemblance to the flagella of *Saronomus capensis* (Kraepelin 1899) (Maury 1982:127–130, figs. 1–8). Six to seven stridulatory ridges on the mesal dorsal aspect of the chelicerae (Fig. 8).

Palpus: tarsal/metatarsal ratio of 3.4:1 (Fig. 3).

Legs: all legs with a single tarsal segment; leg I with no claw and slightly enlarged (bulbous) tarsus; leg IV with ventral spination of 2-2-2-2-1.

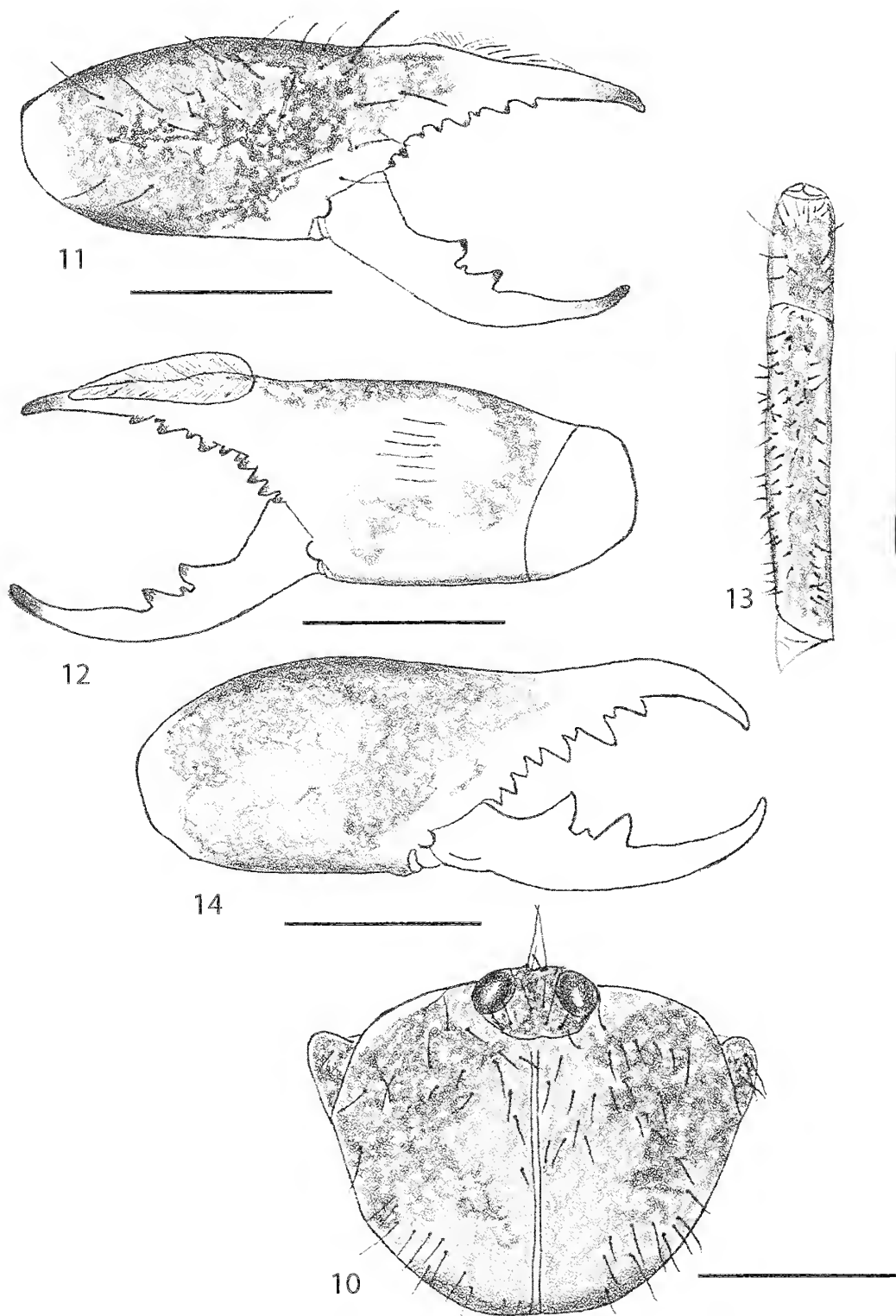
Dimensions.—*Female holotype*: total length 10.0, cheliceral length 5.0, cheliceral width 1.7, propeltidium length 1.75, propeltidium width 3.15, palpus length 10.0, first leg length 8.0, fourth leg length unknown (damaged). Ratios: A/CP (cannot be computed), genital operculum length/width 0.5.

Females ($n = 4$): total length 12.0–16.0, cheliceral length 4.4–4.85, cheliceral width 1.37–1.65, propeltidium length 1.8–2.2, palpus length 12.0–16.0, first leg length 10.0–11.0, fourth leg length 16.0–20.0. Ratios: A/CP 7.26–7.48.

Males ($n = 3$): total length 12.5–13.5, cheliceral length 2.5–2.7, cheliceral width 0.88–0.99, propeltidium length 1.7–1.75, propeltidium width 1.8–2.2, palpus length 12.5–13.5, first leg length 9.0, fourth leg length 17.0–19.0. Ratios: A/CP 10.3–11.7.

Chinchippus viejaensis new species
(Figs. 9–14)

Material examined.—*Types*: PERU: Ica Region: male holotype, Isla La Vieja, Reserva Nacional de Paracas,



Figures 10–14.—*Chinchippus viejaensis*. Male holotype and female allotype, Peru: Isla La Vieja, 15 September 2003, A. Catenazzi. 10–13. Male holotype: 10. Propeltidium, dorsal; 11. Right chelicera, ectal; 12. Right chelicera, mesal; 13. Palpal tarsus, metatarsus, dorsal. 14. Female allotype, right chelicera, ectal. Scale bars = 1 mm.

14°26'28.4"S, 76°12'28.4"W, 230 m, 15 September 2003, A. Catenazzi (DMNS). Allotype female collected with holotype (MUSM).

Etymology.—Named for the type locality, Isla La Vieja, Peru.

Diagnosis.—This species can be differentiated from *C. peruvianus* by its darker coloration, smaller size, and differences in cheliceral dentition (compare Figs. 7 and 11).

Description.—*Male holotype*: Color: pale mottled violet to dark violet-brown overall; palpal tarsus, metatarsus, tibia, and

Table 1.—Average number of *Chinchippus peruvianus* captured per pitfall trap near sandy and muddy beaches at Paracas Bay between 6–9 January 2003. Position = distance from the mean high tide level. Traps = number of pitfall traps. No males were captured in pitfall traps.

Position	Traps	Females	Immatures
5 m	27	0.11 ± 0.06	0.04 ± 0.04
10 m	27	0.07 ± 0.05	—
15 m	27	0.07 ± 0.05	0.04 ± 0.04
Total	81	0.09 ± 0.03	0.02 ± 0.02

apical two thirds of the femur dark violet-brown dorsally, creamy white ventrally; legs I and II dusky brown and violet-brown at the tibia-femur; legs III and IV violet-brown dorsally on tibia, fibula, and apical portion of tarsus; propeltidium darker violet-brown with a very pale ovate area and a median thin, pale stripe extending from eye tubercle to the posterior of the propeltidium (Figs. 9, 10); chelicerae mottled violet-brown (Figs. 9, 11); abdomen with dorsal violet-brown patches on each sternite dorsally (Fig. 9); malleoli white.

Chelicera: fondal teeth three of equal size, fixed finger dentition 1-P-M-1-A, movable finger dentition P-1-A. Six to seven stridulatory ridges found on posterior mesal surface of chelicerae (Figs. 11, 12). Flagellum of *C. viejaensis* similar to *C. peruvianus* with a slightly narrow anterior opening and perhaps a more medial attachment above the primary tooth. No setae or fringe is visible. The cheliceral dentition pattern shows some similarity to *Ammotrechula gervaisii* (Pocock 1895) (Roewer 1934:600) but has no mesal tooth and no fringed flagellum. Palpus: metatarsus/tarsus ratio 3:1; no spine-like setae (Fig. 13).

Legs: leg I with no claw; leg IV with 2-2-1 spine-like setae on the ventral aspect of the tarsus and 2-2-1-1 on the metatarsus.

Female allotype: Color: very similar to the male with the abdominal tergites a lighter color (Fig. 9). The median pale ovate area of the propeltidium is lighter in the female. Leg III femur creamy white.

Chelicera: fixed finger dentition P-1-M-1-A; movable finger P-1-A; fondal teeth III, I, II, IV ectally and mesally; 5–6 stridulatory ridges on the dorsal mesal aspect (Fig. 12).

Palps: metatarsi/tarsi ratio of 2.5:1.

Legs: leg IV with 2-2-1 spine-like setal pattern on ventral aspect of the tarsus and 2-2-1-1 on the metatarsus.

Abdomen: genital operculum similar to *C. peruvianus* with a deep central cavity forming the entrance to the genital orifice.

Dimensions.—*Male holotype*: length 10.0, cheliceral length 2.35, cheliceral width 0.97, propeltidium length 1.54, propeltidium width 2.02, palpus length 10.0, first leg length 7.0, fourth leg length 8.0. Ratios: A/CP 6.84. *Female allotype*: total length 11.0, cheliceral length 2.75, cheliceral width 1.04, propeltidium length 1.51, propeltidium width 2.27, palpal length 7.0, first leg length 6.0, fourth leg length 6.5. Ratios: A/CP 5.64.

TAXONOMIC REMARKS

Previous to this study, *Chinchippus* was a monotypic genus based on a single female specimen. The identification of the associated male and a second species supports Chamberlin's (1920) erection of this genus. These two species are in the subfamily Saronominae based on tarsal segmentation of the

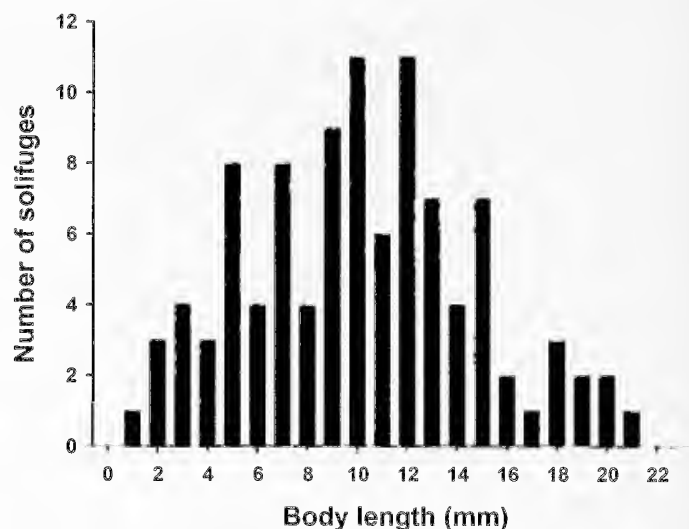


Figure 15.—Size distribution of *Chinchippus peruvianus* ($n = 101$ individuals) at Cangrejal, Paracas Bay, Peru between 26–28 March 2003.

4th leg and the flagellar structure. These characters differentiate the species in the Saronominae from all species currently placed in the Ammotrechinae. The genital opercula of the two species of *Chinchippus* are very similar and differ from other members of the subfamily Saronominae or Ammotrechinae.

ECOLOGICAL RESULTS AND DISCUSSION

Chinchippus peruvianus.—Murphy (1925) collected the holotype in a building of the Compañía Administradora del Guano on the Islas Chinchas and reported that individuals hunt for invertebrates attracted to a light source at night. We made most of our collections and observations on the natural history of *C. peruvianus* at the Paracas Peninsula and on Isla Sangayán. The species appeared to be extremely abundant along a 2 km stretch of shelly beach near the southern end of Paracas Bay (Catenazzi & Donnelly 2007a, b), where individuals could easily be found by lifting rocks, empty shells, and dried marine wrack near shore. At Isla Sangayán, we observed *C. peruvianus* under rocks and carcasses of South American sea lions (*Otaria flavescens* Péron 1816).

Results of the January pitfall trapping near sandy/muddy beaches of Paracas Bay (Table 1) suggest that *C. peruvianus* was more frequent along shelly beaches (see results in Catenazzi & Donnelly 2007a) than it was along sandy or muddy beaches (see below for data from gecko stomach content analyses in support of this hypothesis). Body length distribution for individuals captured on shelly beaches during March 2003 (Fig. 15) averaged 9.4 ± 0.4 mm for the population including immatures ($n = 101$); the maximum body length was 20.2 mm for a female.

Chinchippus peruvianus was found in stomach contents of *P. angustigutis* from most sites in the Paracas Peninsula and from all sites on Isla Sangayán (Tables 2, 3; Fig. 1). Note that the site with 100% frequency of occurrence of *C. peruvianus* (gull colony on Sangayán) was based on the stomach contents of only three geckos. At the Paracas Peninsula, near-shore sites along Paracas Bay and Lagunillas Bay had the highest frequencies of occurrence, possibly because of the large amount of beach-cast macro-algae supporting abundant

Table 2.—Spatial variation in the frequency of occurrence of *Chinchippus peruvianus* in stomach contents of the gecko *Phyllodactylus angustidigitus* in 10 sites of the Paracas Peninsula, Peru between March and December 2003. See Fig. 1 for site locations. Geckos = number of stomach contents examined; Occurrence = frequency of *C. peruvianus* in the geckos' stomach contents; Prey items = number of all prey items in the geckos' stomach contents; Frequency = frequency of *C. peruvianus* relative to the number of prey items.

Site	Geckos	Occurrence	Prey items	Frequency
<i>Paracas Peninsula</i>				
Cangrejal	127	22.8% (29)	607	5.8% (35)
La Aguada	43	4.7% (2)	383	0.5% (2)
Sequión	33	12.1% (4)	218	1.8% (4)
Yumaque	17	— (0)	81	— (0)
Talpo	41	— (0)	171	— (0)
Lagunillas	41	9.8% (4)	235	2.1% (5)
Playa roja	24	8.3% (2)	166	1.2% (2)
Los Viejos (beach)	54	— (0)	421	— (0)
Los Viejos (desert)	38	5.3% (2)	96	2.1% (2)
Arquillo	18	5.6% (1)	123	0.8% (1)
<i>Isla Sangayán</i>				
Lobera	178	1.1% (2)	1408	0.2% (3)
Gull colony	3	100.0% (3)	65	20.0% (13)
Lomas	27	3.7% (1)	164	0.6% (1)
Total	644	7.8% (50)	4138	1.6% (68)

populations of intertidal arthropods and/or because these beaches were easily accessible to both solifuges and geckos. Frequencies of occurrence were low at coastal sites near cliffs (Arquillo, Yumaque, Playa Roja) or sites that are exposed to the ocean (Los Viejos, Talpo), similarly to distribution patterns found in *P. angustidigitus* geckos (Catenazzi & Donnelly, unpublished data). *Chinchippus peruvianus* readily excavates burrows in fine sand when disturbed. The burrowing behavior included biting, raking, and plowing sand at irregular intervals. However, *C. peruvianus* was also found in pebble beaches and in coarse soil where other microhabitats replace burrows (e.g., dried macroalgae, sea lion and seabird carcasses; A. Catenazzi pers. obs.).

Other species of South American solifuges seem to be associated with vegetation cover and soil characteristics: for example Xavier & Rocha (2001) detected a preference of *Mummucia mauryi* Rocha (in Xavier & Rocha 2001) for areas covered by *Opuntia inamoena* (Cactaceae) during the dry season, whereas Rocha & Carvalho (2006) and Martins et al. (2004) noted that white sandy soils where solifuges can easily excavate their burrows may facilitate colonization by *Mummucia taiete* Rocha & Carvalho 2006 and *M. coaraciandu*

Pinto-da-Rocha & Rocha 2004 respectively. In the case of *C. peruvianus* (as well as *C. viejaensis*, see below), vegetation cover is unlikely to explain distribution patterns because it is extremely scarce and absent at most sites. Island and coastal habitats colonized by the two *Chinchippus* also differ widely in soil types (A. Catenazzi, pers. obs.; see habitat descriptions). The higher frequency of occurrence of these solifuges in places that receive marine-derived energy and nutrients, such as beaches with stranded marine macroalgae colonized by arthropods or insular seabird colonies with arthropod scavengers and ectoparasites suggests that food availability in the hyper-arid Peruvian coastal desert may explain distribution patterns.

Seasonal activity can be inferred from results of the geckos' stomach contents, by assuming that the feeding preference of geckos did not vary seasonally. Solifuges at Paracas Bay were most frequent in the geckos' stomachs during the austral summer (Table 3), and their frequency of occurrence with respect to the total number of prey items from March to December 2003 (including data from December 2004) followed a polynomial curve ($y = 0.42x^2 - 6.8x + 27.7$, $R = 0.81$) with a minimum predicted value for August (0.3%

Table 3.—Seasonal variation in the frequency of occurrence of *Chinchippus peruvianus* in stomach contents of the gecko *Phyllodactylus angustidigitus* at Paracas Bay, Peru during March–December 2003. See Fig. 1 for site location and Table 2 for table headings; * includes 15 stomach contents collected in December 2004.

Month	Geckos	Occurrence	Prey items	Frequency
March	12	25.0% (3)	40	10.0% (4)
April	35	20.0% (7)	130	7.7% (10)
May	43	18.6% (8)	176	5.7% (10)
June	27	18.5% (5)	188	2.7% (5)
July	9	— (0)	35	— (0)
August	16	6.3% (1)	143	0.7% (1)
September	3	— (0)	89	— (0)
October	8	25.0% (2)	65	3.1% (2)
November	13	— (0)	112	— (0)
December*	19	26.3% (5)	55	9.1% (5)
Total	170	18.2% (31)	990	3.7% (37)

Table 4.—Spatial variation in the frequency of occurrence of *Chinchippus viejaensis* in stomach contents of the gecko *Phyllodactylus angustidigitus* in four sites of Isla La Vieja, Peru. See Fig. 1 for site locations and Table 2 for table headings.

Site	Geckos	Occurrence	Prey items	Frequency
AB	22	54.5% (12)	449	3.6% (16)
AC	19	15.8% (3)	96	3.1% (3)
Pan de Azúcar				
Beach	36	2.8% (1)	224	0.4% (1)
Zona guanera	14	7.1% (1)	182	0.5% (1)
Total	91	18.7% (17)	951	2.2% (21)

frequency of occurrence). This seasonal activity contrasts with the phenology described by Martins et al. (2004) for *M. coaraciandu* in the Brazilian Cerrado, where surface activity based on pitfall traps was negatively correlated with monthly temperature. However, higher temperatures in the Cerrado were associated with higher rainfall, which could also influence solifuge activity. Rainfall in Paracas is negligible throughout the year, but average night temperatures can be low in the austral winter and could limit solifuge activity.

The diet of *C. peruvianus* is dependent upon marine sources of energy and nutrients. In the case of supratidal populations, such as those in Paracas Bay (Tables 3 and 4), solifuges rely on intertidal algivores for their diet (Catenazzi & Donnelly 2007a). The beach hopper *Transorchestia chilensis* (Amphipoda, Talitridae) was the most common prey item based on field observations (5 out of 10 feeding events). Analyses of stable carbon isotopes also suggested that these beach hoppers were an important prey item for *C. peruvianus* (Catenazzi & Donnelly 2007a, b).

Insular solifuge populations likely feed on ectoparasites and other arthropods found in detritus or on the carcasses of seabirds and pinnipeds because the Islas Chinchas (type locality of *C. peruvianus*) are entirely devoid of vegetation, and Isla Sangayán has scant vegetation that occupies a tiny fraction of the island (the site Lomas in Fig. 1); both islands are mostly cliff-bound. For solifuge populations near the *Otaria flavescens* colony on Isla Sangayán (site Lobera in Fig. 1), arthropod scavengers of pinniped carcasses are likely to be important dietary items, as suggested by the high carbon and nitrogen stable isotope values (albeit only two individuals were analyzed, with $\delta^{13}\text{C} = -14.64\text{‰}$ and 14.89‰ and $\delta^{15}\text{N} = 24.33\text{‰}$ and 25.58‰ ; A. Catenazzi, unpubl. data). Nitrogen isotopic values increase on average by 3.4‰ for each trophic interaction and therefore can be used to estimate the trophic position of an organism (Post 2002). Nitrogen isotopic values of *O. flavescens* on Sangayán average $17.44 \pm 0.35\text{‰}$ (Catenazzi & Donnelly 2008); therefore, isotopic values of *C. peruvianus* are consistent with the idea that solifuges feed on scavengers of *O. flavescens*; (i.e., that they are two trophic positions above *O. flavescens*).

Natural predators of *C. peruvianus* at the Paracas Peninsula and Sangayán include, in addition to *P. angustidigitus*, the scorpion *Brachistosternus ehrenbergii* (Gervais 1841), the spider *Odo* sp. (Zorididae), as well as conspecific individuals. Cannibalism is likely to be common, because these solifuges occur at high density in the first meters from shore. We observed cannibalism in the field on two occasions, and all

captive encounters of pairs of *C. peruvianus* resulted in one individual devouring the other one.

The tsunami that followed a 7.8 magnitude earthquake on 15 August 2007 modified the coastal landscape in Paracas Bay. High waves removed many of the supralittoral dunes where *C. peruvianus* specimens had been collected for this study. It is possible that the flooding of the supratidal areas caused a decline in local populations because Catenazzi & Donnelly (2007a) noted that most *C. peruvianus* are found in the supratidal zone within 1 m from the high mean tide level. However, *C. peruvianus* could recolonize supratidal areas from sections of beach that were protected from the tsunami by a steeper slope of the beach and/or by the presence of rocks and other topographic features.

Chinchippus viejaensis.—This species has only been collected from Isla La Vieja (also called Isla Independencia) in central Peru. This island (area 60.86 ha) is located in Independencia Bay, approximately 6 km west of the mainland and 1.6 km north of a smaller island, Santa Rosa (Fig. 1). Both La Vieja and Santa Rosa are guano islands where hundreds of thousands of seabirds, mainly guanay cormorants (*Phalacrocorax bougainvillii* Lesson 1837) and Peruvian boobies (*Sula variegata* Tschudi 1843), used to congregate. At the time of our visits between July and November 2003, La Vieja did not have any breeding colony of these two guano bird species. However, the upper parts of the island were interspersed with nests of kelp gulls (*Larus dominicanus* Lichtenstein 1823) and Peruvian diving-petrels (*Pelecanoides garnotii* Lesson 1828). Most specimens of *Chinchippus viejaensis* were collected in pitfall traps and stomach contents of the gecko *P. angustidigitus* from a small ridge on the southern slope of the island (type locality, site AB on Fig. 1). The slope measures $\sim 12^\circ$ and is exposed towards the south. The ground is covered with coarse pebbles (16–32 mm grain size) interspersed with a few granitic outcrops. No plants grow along the ridge or neighboring areas; however, a thin lichen crust covered some rocks along the top of the ridge. Predominant winds carry ocean aerosols and moisture towards the ridge, which may explain the presence of lichens in an otherwise unproductive environment. During our November visit, we observed many nests of kelp gulls; most nests had been built between rocks along the ridge.

Based on our observations, we can document predation of this solifuge by *P. angustidigitus* only. *Chinchippus viejaensis* was found in 18.7% of the gecko stomach contents from the entire island, and in 54.5% (12 in 22) of the stomach contents collected at the AB site (Fig. 1, Table 4). Additional sampling locations (Fig. 1) included the western slope of the island (site AC), the beach near Pan de Azúcar, and the guano area north of Pan de Azúcar. Site AC is similar to site AB in being a barren slope with granitic outcrops and seabird nests. However, this slope is steeper (19°) and exposed to the west. The ground is composed of fine to medium pebbles with some large rocks and several granitic outcrops. Subterranean nests of Peruvian diving-petrels occupy areas of very fine pebbles and coarse sand, whereas nests of kelp gulls (much less frequent than at the AB site) are located among rocks in the granitic outcrops, along with very few plants of *Solanum murphyi* I.M. Johnst. (four plants within a 2.25-ha quadrat plot). The beach near Pan de Azúcar is made of coarse pebbles

Table 5.—Seasonal variation in the frequency of occurrence of *Chinchippus viejaensis* in stomach contents of the gecko *Phyllodactylus angustidigitus* at Isla La Vieja, Peru. See Fig. 1 for location and Table 2 for table headings.

Month	Geckos	Occurrence	Prey items	Frequency
July	35	14.3% (5)	403	1.2% (5)
September	38	18.4% (7)	376	2.4% (9)
November	18	27.8% (7)	172	4.1% (7)
Total	91	18.7% (17)	951	2.2% (21)

frequently littered with marine wrack including kelp and crustacean carcasses. The ground adjacent to the beach is a gentle slope that abuts on a shallow depression to the northwest of Pan de Azúcar beach. Much of this slope had been used by guanay cormorants and Peruvian boobies for nesting ground because at the time of our visit, the ground was covered with ~30 cm of guano. Similarly, guano birds once occupied the guano area to the north of the mentioned shallow depression.

It is likely that invertebrates feeding upon seabirds or consuming detritus associated with seabird activity (e.g., regurgitates, feathers, guano, etc.) are important prey items for this solifuge species because the extreme aridity and scant primary productivity of the island supports very few herbivores. In support of this hypothesis, the occurrence and frequency of *C. viejaensis* in the gecko stomach contents almost doubled at the onset of the breeding season of kelp gulls in November (Table 5).

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LITERATURE CITED

- Alpers, C.N. & G.H. Brimhall. 1988. Middle Miocene climatic change in the Atacama Desert, northern Chile: evidence from supergene mineralization at la Escondida. *Geological Society of America Bulletin* 100:1640–1656.
- Brookhart, J.O. & P.E. Cushing. 2002. New species of Eremobatidae (Arachnida, Solifugae) from North America. *Journal of Arachnology* 30:84–97.
- Brookhart, J.O. & P.E. Cushing. 2004. The systematics of the *Eremobates scaber* group (Solifugae, Eremobatidae). *Journal of Arachnology* 32:284–312.
- Brookhart, J.O. & M.H. Muma. 1981. The pallipes species-group of *Eremobates* Banks (Solpugida: Arachnida) in the United States. *Florida Entomologist* 64:283–308.
- Brookhart, J.O. & M.H. Muma. 1987. *Arenotherus*, a new genus of Eremobatidae (Solpugida) in the United States. Privately published by the authors, Cherry Creek High School Print Shop, Englewood, Colorado, USA. 18 pp.
- Catenazzi, A. & M.A. Donnelly. 2007a. The *Ulva* connection: marine green algae subsidize terrestrial consumers in coastal Peru. *Oikos* 116:75–86.
- Catenazzi, A. & M.A. Donnelly. 2007b. Role of supratidal invertebrates in the decomposition of beach-cast green algae (*Ulva* sp.). *Marine Ecology Progress Series* 349:33–42.
- Catenazzi, A. & M.A. Donnelly. 2008. Sea lions (*Otaria flavescens*) as hosts of the common vampire bat (*Desmodus rotundus*). *Marine Ecology Progress Series* 360:285–289.
- Chamberlin, R.V. 1920. South American Arachnida, chiefly from the guano islands of Peru. The Brooklyn Institute of Arts and Sciences, *Science Bulletin* 3:35–44.
- Craig, A.K. & N.P. Psuty. 1968. The Paracas Papers. Reconnaissance Report. Studies in Marine Desert Ecology. Publication of the Department of Geography, Florida Atlantic University 1:1–196.
- Dietrich, W.E. & J.T. Perron. 2006. The search for a topographic signature of life. *Nature* 439:411–418.
- Environmental Resources Management. 2002. Estudio de impacto ambiental del proyecto Planta de fraccionamiento de LGN e instalaciones de carga y alternativa cañería submarina en Playa Loberío, Pisco, Ica, Perú. - Environmental Resources Management.
- Martins, E.G., V. Bonato, G. Machado, R. Pinto-Da-Rocha & L.S. Rocha. 2004. Description and ecology of a new species of sun spider (Arachnida: Solifugae) from the Brazilian Cerrado. *Journal of Natural History* 38:2361–2375.
- Maury, E.A. 1982. Solifugos de Colombia y Venezuela (Solifugae, Ammotrechidae). *Journal of Arachnology* 10:123–143.
- Muma, M.H. 1951. The arachnid order Solpugida in the United States. *Bulletin of the American Museum of Natural History* 97:35–141.
- Muma, M.H. 1976. A review of solpugid families with an annotated list of western hemisphere solpugids. Publication of the Office of Research, Western New Mexico University, Silver City 2:1–33.
- Muma, M.H. & J. Brookhart. 1988. The *Eremobates palpisetulosus* species-group (Solpugida: Eremobatidae) in the United States. Privately published by the authors, Cherry Creek High School Print Shop, Englewood, Colorado, USA. 65 pp.
- Murphy, R.C. 1925. Bird Islands of Peru: the Record of a Sojourn on the West Coast. Putnam and Sons, New York. 362 pp.
- Polis, G. & S.D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land. *American Naturalist* 147:396–423.
- Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718.
- Rocha, L.S. & M.C. Carvalho. 2006. Description and ecology of a new solifuge from Brazilian Amazonia (Arachnida, Solifugae, Mummuciidae). *Journal of Arachnology* 34:163–169.
- Roewer, C.F. 1934. Solifugae, Palpigradi. In *Klassen und Ordnungen des Tierreichs. 5: Arthropoda. IV: Arachnoidea*. (H.G. Bronn, ed.), Vol. 5 (IV) (4) (4–5):481–723, Akademische Verlagsgesellschaft M.B.H., Leipzig.
- Tarazona, J. & W. Arntz. 2001. The Peruvian coastal upwelling system. Pp. 229–243. In *Coastal Marine Ecosystems of Latin America*. (U. Seeliger & B. Kjerfve, eds.). Springer-Verlag, Berlin.
- Xavier, E. & L.S. Rocha. 2001. Autoecology and description of *Mummucia mauri* (Solifugae, Mummuciidae), a new solifuge from Brazilian semi-arid Caatinga. *Journal of Arachnology* 29:127–134.

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Estimating biomass of Neotropical spiders and other arachnids (Araneae, Opiliones, Pseudoscorpiones, Ricinulei) by mass-length regressions

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Abstract. We sampled 505 specimens of 7 arachnid orders (313 Araneae, 65 Opiliones, 111 Pseudoscorpiones, 10 Ricinulei, 3 Schizomida, 1 Thelyphonida, 2 Scorpiones) in natural forest and agroforestry sites in central Amazonia to analyze fresh and dry mass to body length relations. The low number of schizomids, scorpions, and thelyphonids did not allow statistical analyses, but the raw data are given, because these represent the first data published for these groups from Amazonia. For all other orders general mass-length relationships for ecological studies were determined. Non-linear regressions with a power model proved to describe the relations very well and are highly significant for all taxa and groups analyzed. The resulting equations can thus be used to estimate biomass of large samples of arachnids from Amazonia based on individual body length measurements. Linear regressions of mass to length with log-transformed data also described the relation adequately, but using the resulting equations to estimate biomass of the whole spider sample caused a higher bias. This is because small biases of mass-length relation of the largest spider individuals are exponentiated. However, linear regressions behaved better for spiders smaller than 8 mm. The ratio of dry to fresh mass was around 0.3 for spiders; 0.4 for pseudoscorpions, schizomids, and thelyphonids; 0.44 for opilions; and 0.53 for Ricinulei. A second sample of 99 spiders from a South Brazilian Atlantic Forest revealed similar mass-length relations, but a different dry to fresh mass ratio. For spiders, the usefulness of general equations to determine the biomass of bulk samples from ecological studies with certain precision requirements was further explored by using the equations from the two datasets crosswise, regarding the resulting bias and by applying equations to a further dataset from an ecological investigation. In conclusion and accordance to former studies, general equations derived from mass-length regressions of bulk samples including many specimens of different families and guilds are appropriate for an estimation of the biomass of bulk samples from ecological studies. Equations from mass-length regressions from the literature, resulting from spider samples in temperate regions, should not be used to estimate biomass of samples from neotropical spider assemblages, especially when absolute biomass is of interest and when precision is required. They underestimate biomass of tropical assemblages due to a strong bias in mass-length relation of tropical spiders larger than 10 mm. Depending on the distribution of large spiders in samples, considerable biases in single samples could affect ecological analyses.

Resumo. Analisamos as relações entre comprimento corporal e massa fresca e seca de 505 espécimes de sete ordens de aracnídeos (313 Araneae, 65 Opiliones, 111 Pseudoscorpiones, 10 Ricinulei, 3 Schizomida, 1 Thelyphonida, 2 Scorpiones) coletados em florestas e agroflorestas na Amazônia Central. Devido ao número baixo de Schizomida, Scorpiones e Thelyphonida nenhuma análise estatística foi possível e os dados brutos são apresentados a serem os primeiros dados publicados destes grupos para a Amazônia. Para as outras ordens análises de regressão foram feitas. Regressões não-lineares de modelo potencial demonstraram excelente descrição para as relações, sendo altamente significativas para os táxons e grupos analisados. Os coeficientes obtidos nestas regressões poderão servir de base para o cálculo de biomassa em amostras da Região Amazônica que contenham grande número de aracnídeos, utilizando-se como medida somente o comprimento total de cada indivíduo. Utilizando-se dados logaritmicamente transformados, regressões lineares de massa-comprimento também descreveram adequadamente a relação. Todavia a utilização destes coeficientes, para estimar exclusivamente a biomassa da amostra total de aranhas, apresentou resultados tendenciosos em função do efeito forte da relação exponencial a desvios pequenos em aranhas de grande porte. Regressões lineares apresentaram um comportamento estatístico mais favorável apenas para aranhas com menos de 8 mm de comprimento corporal. A relação obtida para massa seca em relação à massa fresca foi de cerca de 0.3 para aranhas, cerca de 0.4 para Pseudoscorpiones, Schizomida e Thelyphonida, 0.44 para Opiliones e 0.53 para Ricinulei. Uma segunda amostragem de 99 aranhas na região meridional da Mata Atlântica brasileira revelou relações de massa-comprimento similares, porém, com uma relação diferenciada de massa seca à massa fresca. Para a ordem de aranhas a utilidade de equações gerais para a determinação da biomassa de amostras ecológicas com devida precisão foi analisada aplicando coeficientes resultando de amostragens de outras regiões. Concluímos que coeficientes de regressões de massa-comprimento são apropriados para uso em relação à assembléia inteira de aracnídeos, desde que as amostras contenham espécimes de várias famílias e guildas diferentes. Os coeficientes obtidos na regressão da grande amostragem da Região Amazônica podem ser usadas para a assembléias de aranhas da Mata Atlântica, porém não é aconselhável uso recíproco, mais especificamente para estimativas de massa seca. A utilização de coeficientes de regressões de massa-comprimento disponíveis atualmente na literatura, resultante de amostragens em regiões temperadas, deveria ser evitada para a estimativa de biomassa em amostras de assembléias de aranhas neotropicais. Estes coeficientes subestimam a biomassa de assembléias tropicais devido a uma grande distorção na relação entre massa e comprimento corporal em aranhas maiores do que 10 mm. Desta maneira análises ecológicas podem ser altamente influenciadas pela distribuição de grandes aranhas entre as amostras individuais com distorção dos resultados.

Keywords: Arachnida, mass-length relationship, Brazil

Biomass data (in the sense of the weight of living animals per unit area, Bornebusch 1930; Edwards 1966) for arthropods are needed in many ecological studies, especially when these aim to analyze the role and functions of these abundant animals in ecosystems and food webs. Biomass of soil fauna is of special interest in studies of nutrient cycling involving the role of the fauna in decomposition and organic matter transformation. The importance of soil fauna has long been recognized and their function is also being studied more frequently in Neotropical ecosystems (Lavelle et al. 1997, 2001; Barros et al. 2003, 2006; Mathieu et al. 2004). The context in which we needed to estimate biomass of arachnids and other arthropods was given by two projects in the Brazilian-German research programme SHIFT (Studies on Human Impact on Forests and Floodplains in the Tropics) studying the quantitative contribution of soil fauna to decomposition in central Amazonian natural forests and different agroforestry systems (Höfer et al. 2001; Hanagarth et al. 2004; Martius et al. 2004; Brown et al. 2006).

Biomass can be obtained by direct weighing of individual living arthropods with analytical balances, but this is a very time consuming task and for very active animals it is difficult or impossible to obtain precise data. Certainly direct weighing is not a practical method in the field and for larger samples in laboratories. Most specimens in ecological studies are trapped and killed in fluids such as ethanol and it is difficult to measure preserved animals on a balance. Also, weighing fresh weight of preserved animals may provide incorrect estimations as body weight may be altered during preservation. For most studies dry mass is easier to obtain, but drying specimens or bulk samples to a constant weight, usually at 65° C or more, makes it impossible to later identify them due to their fragility. An alternative method is to use statistically verified relationships of mass with easily measurable body dimensions, such as body length or width, to estimate the biomass of each specimen. Body length might even be measured in the field or estimated with live animals so animals may not even need to be collected. Regressions using a power model (mass = a (size)^b) usually adequately describe mass-length-relations for most arthropods (Rogers et al. 1976, 1977; Schoener 1980; Sample et al. 1993; Edwards 1996). They have also been shown to provide useful data for spiders from temperate regions (Breyer 1967; Norberg 1978; Clausen 1983; Edwards 1996; Henschel et al. 1996a; Lang et al. 1997; Edwards & Gabriel 1998). Spiders and to a lesser extent other arachnids (opilions, pseudoscorpions) are abundant in all terrestrial environments and are often included in functional ecological studies due to their well defined position in the food web as (arthropod) predators and their usefulness to indicate habitat quality (Jocqué 1981; Chen & Wise 1999; Wise et al. 1999; Lawrence & Wise 2000, 2004; Wise 2004). As Henschel et al. (1996a) state, it is useful and possible to use general equations for arachnid orders (e.g., spiders and opilions) to estimate the biomass of single specimens for the whole assemblage, notwithstanding the different species-specific mass-length relationships. They suggest their equations are valid for other regions and habitats in Europe, at least for community studies involving numerous families, genera and species.

Our main interest was to derive an equation for a general relationship to estimate biomass of bulk samples to compare

soil fauna biomass at different sites in tropical South America. Thus we sampled 505 specimens of spiders and other arachnids from one location in central Amazonia and analyzed mass-length relations of this large collection (first data set) in order to obtain valid equations for the biomass estimates we needed for our studies of Amazonian forest and agroforestry systems. We tested whether these equations reliably estimated biomass of bulk samples of spiders or if different equations were necessary for different functional groups (e.g., wandering versus web building spiders), size classes (tiny spiderlings versus large mygalomorphs), or spiders with an extraordinary body shape (like *Micrathena* or *Deinopsis*).

A second sample of spiders (second data set) was obtained from another region and large scale forest ecosystem of Brazil, e.g., in the southern part of the Brazilian Atlantic Forest (Mata Atlântica) and analyzed in the same way. Having two large data sets on spiders at hand and given the numerous data for this arachnid order in the literature, we explored the usefulness and limitations of general equations to determine the biomass of bulk samples from ecological studies with the required precision. This was done in three steps: 1. Determining which biases would be introduced when using equations from outside the Neotropical region for the Amazonian sample; 2. Determining the bias introduced by using the equations from the first data set (Amazonia) for the second data set (Atlantic Forest) and vice versa; 3. Determining the bias introduced by applying different equations for data from one ecological study in Amazonia and one ecological study in the Atlantic forest (application data sets) and looking for an effect of the bias on the conclusions of these studies.

METHODS

Mass-length relations were analyzed using specimens sampled in primary and secondary forests and tree plantations within the area of the Brazilian Agricultural Research Corporation EMBRAPA in central Amazonia near Manaus (02°53'47"S, 59°59'45"W) (first data set). Sampling took place in May 1999 with the aim to obtain as many differently sized and shaped specimens from as many taxa as possible. Specimens were captured alive by hand and stored individually in vials during transport to the laboratory. They were killed by freezing for about one hour and then weighed to obtain fresh mass to the nearest 0.001 mg with a Sartorius MP2 microbalance. Body length, in dorsal view from the anterior edge of the prosoma (excluding chelicerae) to the posterior edge of the opisthosoma (excluding spinnerets), was measured with a graduated eyepiece to the nearest 0.01 mm. Numbers of specimens measured for each order and lower taxonomic levels are given in Table 1 (first data set). Lastly specimens were oven-dried for 24 h at 105° C, cooled to room temperature, and weighed to obtain dry mass. Only three of the ten *Ricinulei* specimens were dried because of their rarity in museum collections. The resulting ratio dry/fresh mass for these specimens was used to calculate the dry mass for the seven other specimens. From three other arachnid orders too few specimens were caught to calculate regressions (Schizomida: 3, Thelyphonida: 1, Scorpiones: 2). Results are presented in Tables 1, 2 and in Figure 3.

A second data set including 99 spiders from a South Brazilian Atlantic Forest (Mata Atlântica) (Reserva do

Table 1.—Number of specimens measured and weighed for length-mass regression, mean and range of body length (minimum and maximum in brackets) from seven arachnid orders.

Order/Infraorder/Family	First data set (Amazonia)		Second data set (Mata Atlântica)	
	Specimens	Length (mm)	Specimens	Length (mm)
Araneae	313	4.83 (0.56–36.0)	99	7.08 (1.35–28.0)
Infraorder Mygalomorphae	43	3.17 (0.78–19.1)		
Infraorder Araneomorphae:				
Amaurobiidae	1		1	8.27
Anapidae	1	1.07		
Anyphaenidae			2	6.87 (6.83–6.92)
Araneidae	8	1.89 (0.81–3.40)	18	5.77 (2.69–10.67)
Corinnidae	11	5.85 (1.85–13.9)	2	4.57 (4.52–4.62)
Ctenidae	74	12.43 (1.30–36.0)	18	16.52 (4.23–28.0)
Deinopidae			1	16.50
Linyphiidae	9	1.60 (1.20–1.90)	1	2.30
Lycosidae			2	16.85 (7.69–26.0)
Mysmenidae			3	1.73 (1.35–2.40)
Ochyroceratidae	24	1.40 (0.56–2.40)	1	1.83
Oecobiidae	2	1.75 (1.70–1.80)		
Oonopidae	68	1.46 (0.67–2.50)	1	2.31
Palpimanidae	4	3.04 (1.52–4.00)		
Pholcidae	8	2.00 (1.07–4.30)	6	2.79 (1.92–3.94)
Pisauridae	2	4.67 (3.96–5.40)	1	4.61
Salticidae	39	3.40 (1.12–6.60)	4	4.86 (3.65–5.77)
Scytodidae	5	2.57 (1.60–3.10)		
Selenopidae			1	5.00
Sparassidae	3	6.00 (5.90–6.10)	2	5.58 (3.56–7.60)
Tetragnathidae			2	5.86 (4.33–7.40)
Theridiidae	5	1.33 (1.00–2.00)	20	3.02 (1.63–10.0)
Theridiosomatidae	3	0.75 (0.62–0.83)	3	1.91 (1.49–2.69)
Thomisidae			1	7.60
Trechaleidae			3	12.53 (5.29–25.0)
Uloboridae			1	5.38
Zodariidae	4	3.60 (2.00–4.50)		
Zoridae			4	4.23 (3.85–4.81)
Opiliones	65	2.12 (0.57–6.90)		
Pseudoscorpiones	111	1.38 (0.86–2.10)		
Ricinulei	10	4.46 (2.10–5.60)		
Schizomida	3	1.62 (1.45–1.88)		
Scorpiones	2	16.30 (3.60–29.0)		
Thelyphonida	1	7.00		

Cachoeira, Antonina, Paraná: 25°25'S, 48°40'W) was obtained in 2007. Spiders (Table 1) were sampled manually at night and during the day along trails in secondary forests. Weighing and measuring procedures were the same as described above.

Tests for the effects of the bias from different equations were done with two application data sets: one from Amazonia, where spiders were sampled from 16 replicate sites of each of 7 different plantation systems (EMBRAPA central Amazonia) by means of large soil cores; and one from the Atlantic Forest, where 10 litter samples (1 m²) were taken in each of three different regeneration stages of a sub-mountain forest (Schmidt et al. 2008). From both collections all spider specimens ($n = 441$ and 276) were individually measured (body length), so that coefficients from different regression equations could be applied to estimate the total biomass per site. Data were analyzed with Statistica 7.1 (StatSoft 2005) and graphs prepared with SigmaPlot® 8.0.2 (SPSS 2002).

RESULTS

Analyses of mass-length relations.—Mass-length relationships (for both fresh and dry mass) for the arachnid orders with enough specimens sampled in the Amazonian habitats (first data set) are very well correlated with a regression model of the non-linear (power) form: $\text{mass} = a (\text{length})^b$. Determination coefficients are usually > 0.9 (Tables 3, 4) and type I error probabilities are very low (< 0.001) for both parameters, with the exception of the rare Ricinulei ($n = 10$, $P = 0.15$ for coefficient a).

The mass-length relationship is almost equally well described with a linear model using logarithmic data for length and weight ($\ln(\text{mass}) = a + b \ln(\text{length})$). Note that power regression results are often presented in double-logarithmic plots, but the model parameters are not the same for a power model calculated on raw data and a linear model calculated on log-transformed data. In our dataset the linear model represents the most abundant small spiders better because

Table 2.—Ratios dry/fresh mass for arachnid orders.

Order		Ratio dry/fresh mass	
Family	Guild	First data set (Amazonia)	Second data set (Mata Atlântica)
Araneae		0.29	0.21
Mygalomorphae	hunting	0.29	
Araneomorphae			
Anyphaenidae	hunting		0.25
Amaurobiidae	hunting		0.12
Corinnidae	hunting	0.29	0.27
Ctenidae	hunting	0.26	0.19
Lycosidae	hunting		0.19
Oonopidae	hunting	0.34	0.19
Oxyopidae	hunting		0.24
Palpimanidae	hunting	0.32	
Pisauridae	hunting	0.28	0.22
Salticidae	hunting	0.28	0.21
Scytodidae	hunters	0.29	
Selenopidae	hunting		0.16
Sparassidae	hunting	0.26	0.19
Thomisidae	hunting		0.18
Trechaleidae	hunting		0.20
Zodariidae	hunting	0.34	
Zoridae	hunting		0.20
Anapidae	web-building	0.24	
Araneidae	web-building	0.25	0.22
Deinopidae	web-building		0.16
Linyphiidae	web-building	0.33	0.19
Mysmenidae	web-building		0.20
Ochyroceratidae	web-building	0.31	0.19
Oecobiidae	web-building	0.29	
Pholcidae	web-building	0.27	0.20
Tetragnathidae	web-building		0.29
Theridiidae	web-building	0.28	0.21
Theridiosomatidae	web-building	0.29	0.18
Uloboridae	web-building		0.18
Opiliones		0.41	
Pseudoscorpiones		0.38	
Ricinulei		0.53	
Schizomida		0.37	
Scorpiones		0.30	
Thelyphonida		0.39	

Table 3.—Regression coefficients (a, b) and coefficient of determination in regressions of fresh mass to body length (left: power model: mass [mg] = a body length [mm]^b, right: linear model: \ln mass [mg] = a + \ln body length [mm] b) for arachnids from Amazonia (first data set) and Mata Atlântica (second data set) (n = sample size, se = standard error, R^2 = coefficient of determination). All regressions are highly significant ($P < 0.001$).

	Power model				Linear model		
	n	a \pm se	b \pm se	R^2	a \pm se	b \pm se	R^2
Mata Atlântica: all Araneae	99	0.066 \pm 0.025	3.160 \pm 0.118	0.98	− 2.166 \pm 0.175	2.872 \pm 0.097	0.90
Amazonia: all Araneae	313	0.169 \pm 0.009	2.899 \pm 0.016	0.99	− 2.058 \pm 0.029	2.980 \pm 0.020	0.99
Araneae < 2.5 mm	225	0.085 \pm 0.010	3.288 \pm 0.081	0.94	− 1.958 \pm 0.037	2.746 \pm 0.053	0.92
Ctenidae	74	0.177 \pm 0.020	2.886 \pm 0.034	0.99	− 1.758 \pm 0.096	2.894 \pm 0.039	0.99
Oonopidae	68	0.131 \pm 0.007	2.682 \pm 0.076	0.94	− 2.039 \pm 0.042	2.666 \pm 0.099	0.96
Hunting spiders	253	0.169 \pm 0.010	2.899 \pm 0.018	0.99	− 2.108 \pm 0.023	3.017 \pm 0.015	0.99
Web-building	60	0.072 \pm 0.011	3.710 \pm 0.114	0.97	− 1.784 \pm 0.092	2.255 \pm 0.169	0.75
Opiliones	65	0.147 \pm 0.028	3.622 \pm 0.105	0.98	− 0.899 \pm 0.048	2.984 \pm 0.060	0.97
Pseudoscorpiones	111	0.156 \pm 0.006	2.453 \pm 0.071	0.92	− 1.892 \pm 0.027	2.515 \pm 0.073	0.91
Ricinulei	10	0.225 \pm 0.146	2.760 \pm 0.387	0.93	− 1.907 \pm 0.192	3.014 \pm 0.130	0.98

Table 4.—Regression coefficients (a, b) and coefficient of determination in regressions of dry mass to body length (left: power model: mass [mg] = a body length [mm]^b, right: linear model: \ln mass [mg] = a + \ln body length [mm] b) for arachnids from Amazonia (first data set) and Mata Atlântica (second data set) (n = sample size, se = standard error, R^2 = coefficient of determination). All regressions are highly significant ($P < 0.001$).

	n	Power model			Linear model		
		a \pm se	b \pm se	R^2	a \pm se	b \pm se	R^2
Mata Atlântica: all Araneae	99	0.0067 \pm 0.005	3.413 \pm 0.245	0.96	- 3.860 \pm 0.224	2.950 \pm 0.092	0.93
Amazonia: all Araneae	313	0.0165 \pm 0.001	3.242 \pm 0.014	0.99	- 3.213 \pm 0.029	2.902 \pm 0.021	0.98
Araneae < 2.5 mm	225	0.028 \pm 0.003	3.180 \pm 0.079	0.94	- 3.121 \pm 0.038	2.680 \pm 0.054	0.92
Ctenidae	74	0.017 \pm 0.002	3.232 \pm 0.029	0.99	- 3.197 \pm 0.096	2.921 \pm 0.039	0.99
Oonopidae	68	0.050 \pm 0.003	2.459 \pm 0.094	0.90	- 3.162 \pm 0.046	2.767 \pm 0.108	0.95
Hunting spiders	253	0.0165 \pm 0.001	3.242 \pm 0.016	0.99	- 3.237 \pm 0.025	2.926 \pm 0.016	0.99
Web-building	60	0.017 \pm 0.003	3.881 \pm 0.123	0.97	- 2.997 \pm 0.093	2.199 \pm 0.172	0.74
Opiliones	65	0.042 \pm 0.009	3.879 \pm 0.119	0.98	- 1.862 \pm 0.049	3.069 \pm 0.062	0.97
Pseudoscorpiones	111	0.057 \pm 0.003	2.589 \pm 0.103	0.86	- 2.967 \pm 0.037	2.771 \pm 0.100	0.87

the few large spiders have a very high influence in the power model (Fig. 1). However the fresh biomass of the whole sample (313 spiders) with a mean length of 4.83 mm when estimated with the power model was closer to the observed biomass (99.8%) as when estimated with the linear model (95.7%). The same is true for dry mass estimation (power: 97.6%, linear: 86.9% of observed mass). Because different bulk samples might predominantly consist of either small or large spiders, often influenced by the sampling method, it might be useful to use either the linear model or the power model. In some cases it might even be useful to split a sample by size and use the linear model for spiders < 8 mm and the power model

for spiders > 8 mm. Therefore, we present the coefficients of both models (Tables 3, 4).

The 313 Amazonian spiders that were measured and weighed represent a large spectrum in terms of size, shape, and taxonomic and functional groups. This dataset includes tiny orb-weavers like Theridiosomatidae and Anapidae; tiny, but long-legged Ochyroceratidae; tiny, but short-legged wandering spiders like Oonopidae; median-sized jumping spiders; very small to large mygalomorphs; large ctenid hunters; as well as large, long-legged pholcids (Table 1). Very few spider specimens (the smallest spider an ochyroceratid, one ctenid, and most of the long-legged ochyroceratids) lay

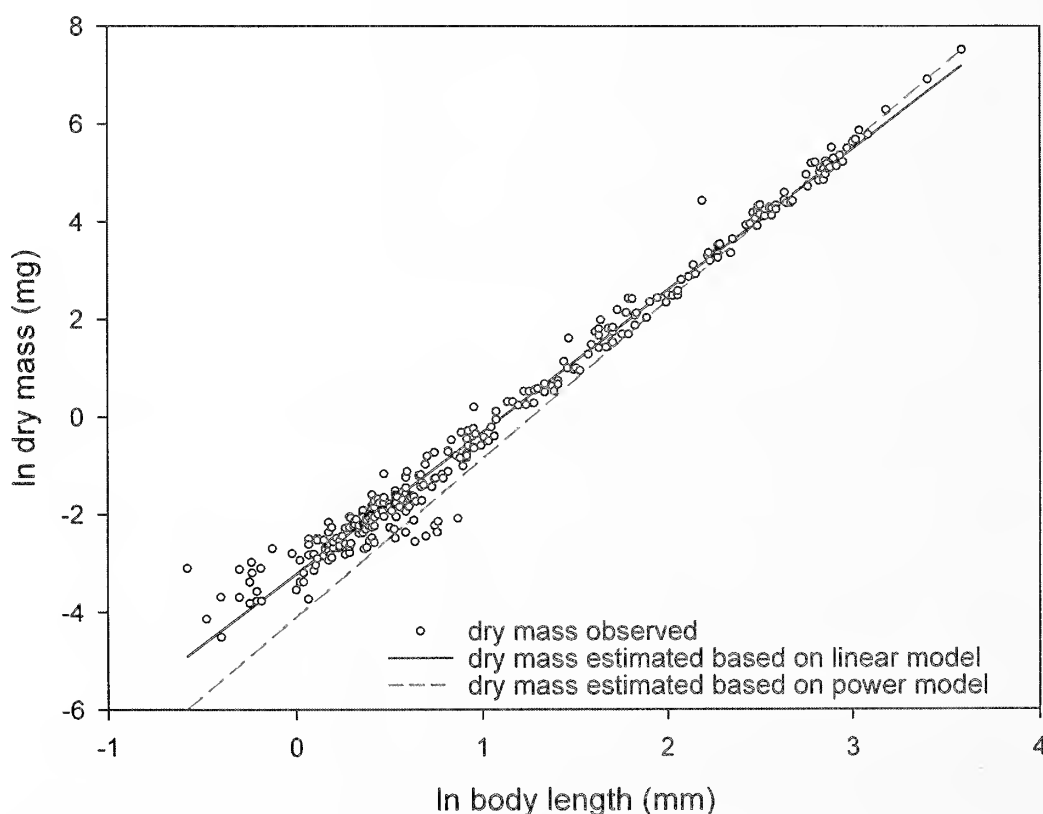


Figure 1.— \ln - \ln plot of dry mass (mg) vs. body length (mm) relationship of spiders in the first data set from Amazonia, showing the bias of a power model regression for small spiders as compared to a linear model regression with a bias for large spiders.

outside the 95% confidence limits of our regressions and their exclusion did not lead to considerable changes in the model parameters.

Nevertheless we calculated separate regressions for small spiders, the families Ctenidae and Oonopidae, the main hunting (or wandering) guilds; and web-building spiders because these groups might be of special interest in ecological studies (see also below); and because they always received high determination coefficients and significances (Tables 3, 4).

The strong correlations in some cases caused very high PRESS values ($> 30,000$ for fresh mass and $> 500,000$ for dry mass vs. length of spiders). The PRESS value (Predicted Residual Error Sum of Squares) is a gauge of how well a regression model predicts new data and often a hint to overfitting of a dataset, resulting in decreased usefulness for other datasets. To test this, we split the whole Amazonian data set by a random procedure in one learn- and one test dataset (cross-validation). For both fresh mass and dry mass the regression line of the test dataset was well inside the 95% confidence limits of the learn dataset. This shows that the strong correlation is not a result of overfitting and consequently the resulting formulae should be useful for an estimation of fresh or dry mass of bulk spider samples from the same region (central Amazonia).

The other three orders (Opiliones, Pseudoscorpiones, Ricinulei) for which regression analyses were possible were much more uniform in size and shape (Table 1). Power and linear models performed equally well and the coefficients are presented in Tables 3, 4. Mass-length relationships of these orders and also the single specimens of Schizomida, Scorpiones, and Thelyphonida are presented in Figure 3.

The mass-length regressions for spiders collected in the Mata Atlântica (second data set) were also strongly correlated and highly significant, but coefficients were slightly different (Tables 3, 4). Only one subadult deinopid and a twig-like *Argyrodes* specimen lay outside the 95% confidence limits, but they did not influence the coefficients of the power model, which produced very good estimates of fresh and dry mass (99.5% of observed value) for the whole sample. The linear model in contrast produced a considerable underestimate of fresh and dry mass (70.2% resp. 73.4%).

Ratio dry/fresh mass.—Fresh mass and dry mass of spiders were strongly correlated ($R^2 = 0.99$, $P < 0.001$) in both data sets; the ratio dry/fresh mass was on average 0.293 ± 0.055 for Amazonian spiders and 0.208 ± 0.06 for spiders from the Atlantic forest. There was no significant difference in ratios for the two main hunting and web-building spider guilds (t -test $P = 0.4$). Anapids (tiny orb weavers) show the smallest ratio (0.24), oonopids and zodariids (small hunters, mostly strongly chitinized) the highest ratio (0.34) (Table 2). The highest variation of dry/fresh mass ratio occurred in the lowest range of body size, which is considered an effect of the decreasing precision of both length and weight measurements with decreasing size of the spiders. There was no correlation between length and the ratio dry/fresh mass.

The ratio dry/fresh for opiliones was 0.44 ± 0.06 and for pseudoscorpions 0.38 ± 0.06 . Both correlations are strong ($R^2 > 0.95$) and highly significant ($P < 0.01$). Mean ratio dry/fresh for the three ricinuleid specimens was 0.53, and for the other arachnids between 0.30 and 0.39 (Table 2).

General usefulness of equations.—Regarding the statistics of mass-length relationships, one certainly gets good estimates of biomass by length measurements for the Amazonian fauna using the coefficients from our equations. But how large would be the bias when using coefficients from other samples for our data or our coefficients for other data?

When using coefficients derived from spider samples from temperate regions (taken from the literature) the estimate of the total biomass of our sample of 313 spiders produced serious biases from the observed mass: 56% (fresh) and 58% (dry mass) with coefficients from the linear model of Edwards & Gabriel (1998; spiders from Massachusetts, USA); 43% (dry mass) with coefficients from the power model of Breymer (1967; spiders from Europe); 25% (dry mass) using the coefficients from the power model of Henschel et al. (1996a; spiders from Germany); 23% (fresh mass) from the power model of Norberg (1978; spiders from spruce in Sweden). These strong biases are caused by the relatively high number of spiders with a length over 12 mm (e.g., Ctenidae) and some very large individuals (24–36 mm) in our samples and the underestimation of these large spiders by formulae from temperate spider faunas (Fig. 2), which only represent spiders up to a length of 10 mm (Henschel et al. 1996a) or 8 mm (Norberg 1978). The equation of Rogers et al. (1977) from spiders (0.7–12 mm) collected from a shrub-steppe in south-central Washington suited our data set better (105% of observed dry mass).

To answer the question whether our equations are generally applicable to samples from spider assemblages in the Neotropics we tested our Amazonian equation on a spider sample (second data set) from another forest Brazilian ecosystem (Mata Atlântica) situated further south, geographically in the subtropics, and vice versa. When applying the Amazonian coefficients, the fresh biomass of the Atlantic Forest spiders was relatively well estimated (113% with power model, 110% with linear model), but the dry mass estimate was considerably overestimated (143% and 121%). This is most probably caused by the lower ratio dry/fresh mass (0.21) for the spiders sampled in the Atlantic Forest in comparison with the spiders from Amazonia (0.29) (Table 2). When using the coefficients from the Mata Atlântica data set for the Amazonian data set the following biases (underestimation) resulted for fresh respectively dry mass: 84.5% / 66.4% by power, 62.6% / 52.4% by linear model.

To obtain an idea of the effect of such biases we used one application data set from Amazonia. Fig. 4 shows box plots with means, medians and variances (percentiles) of spider biomass samples from different plantation systems, calculated with different coefficients. For most (5) systems the biomass of spiders per plot estimated with the equation from Henschel et al. (1996a) was higher than the biomass calculated with our own coefficients and showed comparable relations between medians and means and similar variance. This is due to overestimation of the dominant small spiders (< 4 mm) by the Henschel equation (s.a.). In each of the systems 4 and 6, however, one larger spider (8 mm) was sampled, and these are underestimated by the Henschel equation. In consequence, for these two systems the relative position of the means change depending on the equation used. However, due to the generally high variance of spider abundance between the

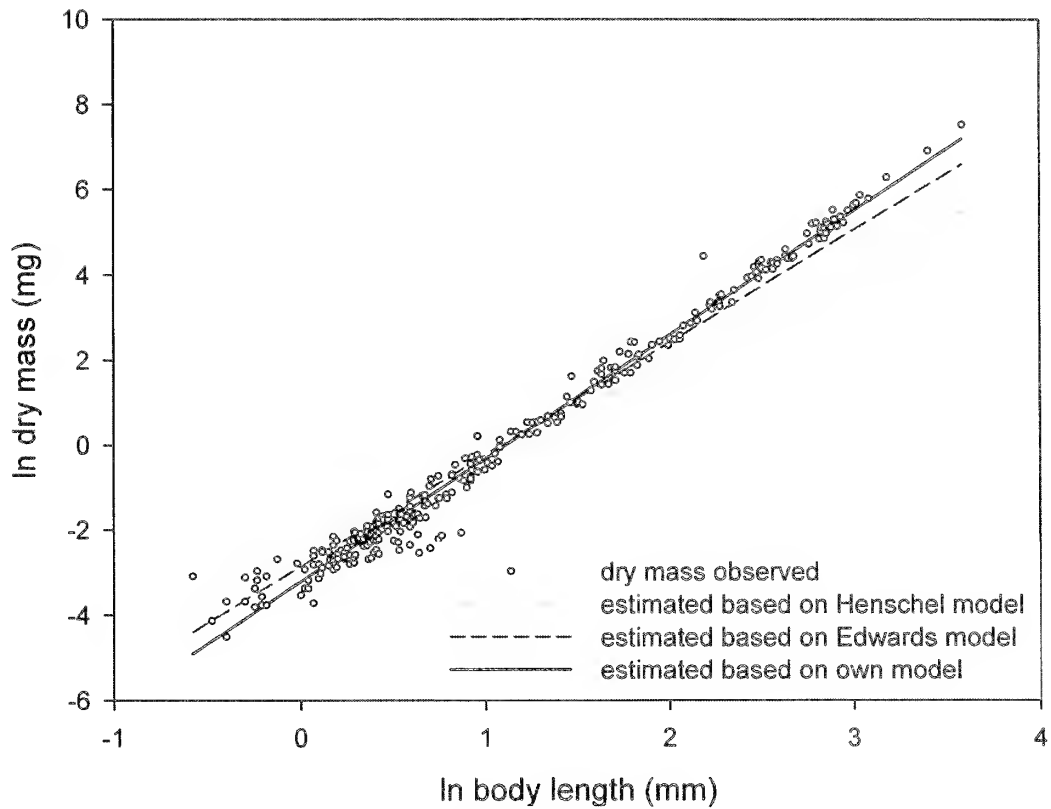


Figure 2.— \ln - \ln plot of dry mass (mg) vs. body length (mm) relationship of spiders in the first data set from Amazonia, showing the bias when using regression coefficients (a, b) from the literature (all linear models).

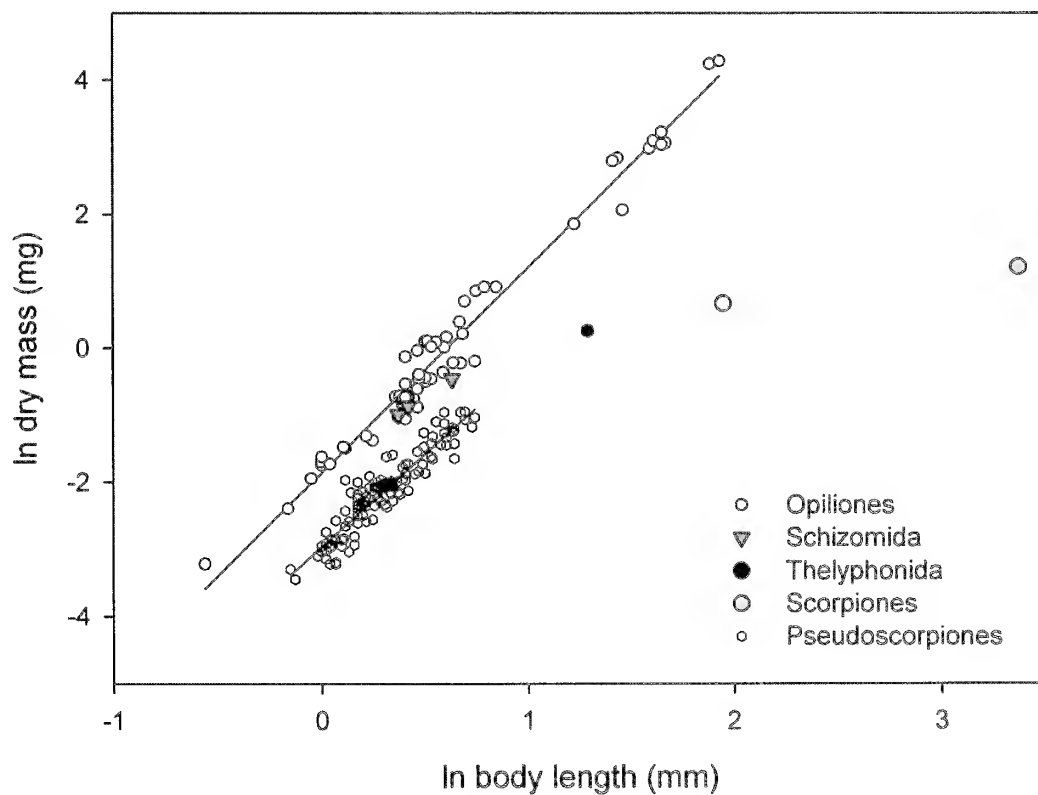


Figure 3.— \ln - \ln plot of dry mass (mg) vs. body length (mm) relationship for other arachnid orders from Amazonia (regression lines for opilionids and pseudoscorpions from linear models).

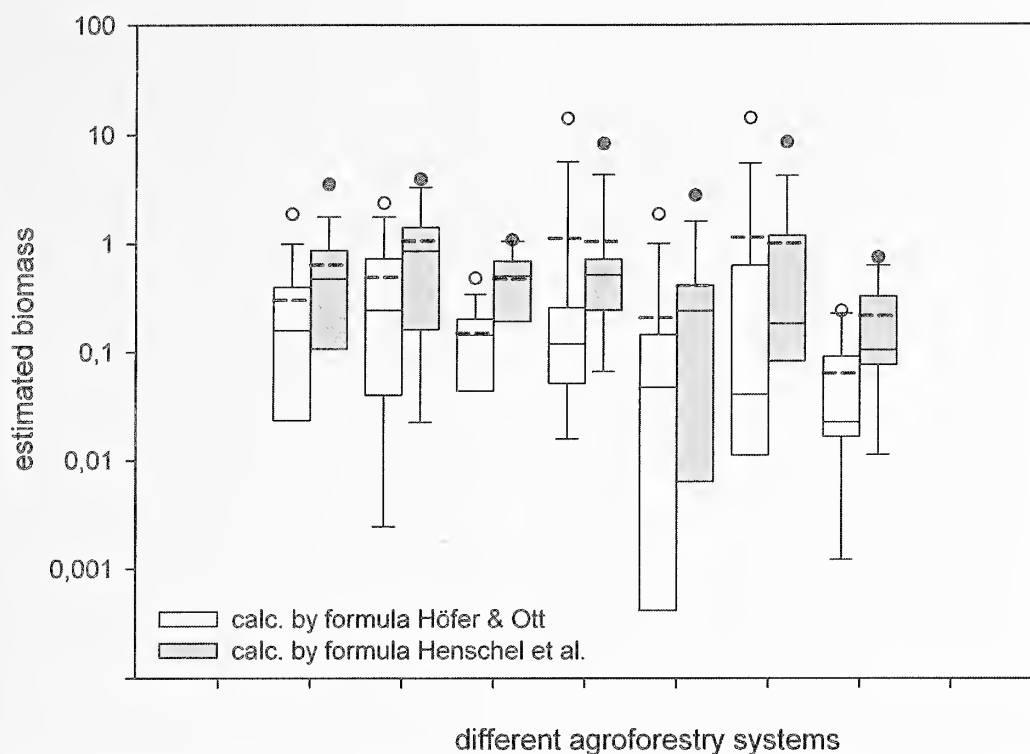


Figure 4.—Estimated total biomass of spiders in samples from seven different agroforestry systems in Amazonia (application data set), showing biases caused by applying regression coefficients originating from a data set from a temperate region in comparison with the coefficients originating from the first (Amazonian) data set. Box plots show the median (thin line), the mean (thick broken line), 25th and 75th percentiles (box), 10th and 90th percentiles (whiskers) and outliers (circles).

replicates there are no significant differences between the systems, no matter if tested on means (ANOVA) or ranks (Kruskal-Wallis) and by both equations.

We also applied the coefficients derived from the Amazonian data set in comparison with the coefficients derived from the Atlantic Forest data set to a second application data set: 30 litter samples taken in three different regeneration stages of an Atlantic sub-mountain forest (Schmidt et al. in press). Mean dry mass values of spiders calculated by the Amazonian formula were 2.8, 5.3, 14.4 mg m^{-2} and calculated by the Atlantic forest formula 1.5, 2.9, 8.6 mg m^{-2} . Biomass values were significantly different (overestimated by the Amazonian formula, paired t -test $P < 0.01$), but ANOVA for the effects of the regeneration stage on biomass gave no significant effect.

DISCUSSION

Mass-length regressions are a formidable solution for estimating biomass without having to destroy the specimens or handle them tediously on a microbalance, which is time-consuming and expensive. Literature and our investigation show clearly that this can be made with one measurement of body length, which can be precisely taken with a micrometer eyepiece or a vernier caliper, even for live arthropods. In view of the very high determination coefficients and very low error probabilities, power regressions of length to estimate fresh or dry mass absolutely satisfy the needs, and no further effort is necessary to estimate volume by measurements of several body dimensions. A model should also not be overfitted (see below) since it would lose its applicability to new datasets.

As mass is expected to be proportional to length cubed, in regression formulae the power (b) in a uniformly proportioned series of animals is expected to be close to 3. The fresh mass of spiders generally followed this relation, whereas dry mass of spiders and fresh and dry mass of opilionids increased with a power greater than 3. For pseudoscorpions, ricinuleids, and the oonopid spiders the power was less than 3. Schoener (1980) explained a power smaller than 3 for insects by a trend of longer species tending to be thinner. For our data set we suppose this to be due to different body densities (mass per volume), because all three groups represent more strongly chitinated rather than thinner animals in comparison to the other groups.

When the aim is to estimate the biomass of bulk samples including many different spider species of different sizes and shapes, one formula can be used for all spiders, although a few very extraordinary shapes (e.g., very long and thin like some *Argyrodes* or *Deinopis*) may lie outside acceptable confidence limits. Especially for tropical soil fauna communities where most specimens are not readily identifiable, often not even to genus or family level, it is desirable, if not necessary, to have one regression equation covering the taxonomic level to which the organisms can be identified (sorted) easily, which most often is the order level for arthropods (Schoener 1980; Sample et al. 1993; Henschel et al. 1996b).

Although not appearing very different, the coefficients given by other authors for estimation of spider biomass from length measurements when applied to our data produced slightly different values for single specimens, which result in consid-

erable biases for bulk samples. The adequate precision of a single mass-length regression depends upon the scientific question, and especially the variance included in the data set (e.g., how many different taxa with different body shapes were included and how strong the abundances vary in reality and in samples). As more mass-length relations of different specimens/species are included, the coefficient of determination R^2 gets smaller, but unless it remains large enough to explain a considerable portion of the variation (> 0.8) and as long as the probability of being wrong in concluding that the coefficient is not zero remains small ($P < 0.05$), the regression model gains in predictability.

In community ecology data sets, the variances in invertebrate abundance between different samples and study sites are usually high (standard deviation $> 100\%$ of the mean) and thus precision of regression factors to calculate the biomass of groups of the community must not be very high, thus allowing relatively fast and rough measures. However, a systematic bias towards certain samples should be avoided. The comparison of the coefficients extracted from the two different models fitting our own data has already shown a possible cause for such a bias: a different proportion of very small or very large spiders in different samples treated with the same equation. In our tests, bias due to the "wrong" equation used for an estimation of biomass did not produce different ecological results. If no equation for the spider assemblage of interest is available, coefficients from an equation based on samples from other regions can be used if the size distributions do not differ strongly, which is obviously the case comparing spider assemblages from temperate and tropical regions. Attention must be given to individual, very large spiders in a sample, which in addition to its already problematic outlier position can produce a king-size bias due to the power effect of the regression. But this should be resolved by statistical procedures in the ecological study.

We have shown that it is difficult if not impossible to estimate biomass from different studies (regions) using the same equation and compare the absolute values. Even within the Neotropical rainforest realm, considerable bias can result from the estimation with non-autochthonous coefficients.

We conclude from our results that our equations from the Amazonian sample are useful for biomass estimation of bulk arachnid samples from ecological studies in Amazonian rainforests and, with some restrictions, also for other neotropical forest spider assemblages. As these are often rich in species, which are represented by several developmental stages, it is valuable to have an idea of the distribution of size classes in the samples. If a wide range of sizes is represented, including spiders larger than 15 mm, the coefficients of the power functions should be used. If only smaller spiders were collected, which is often the case in soil or litter samples, the coefficients of the linear models would be more adequate or the equation resulting from the subsample of spiders < 2.5 mm should be used. We also present the coefficients for specific (abundant) taxa (ctenids, oonopids) and the guilds of hunting and web-building spiders, which can be used in studies of these specific groups.

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LITERATURE CITED

- Barros, E., J. Mathieu, S.C. Tapia-Coral, A.R.L. Nascimento & P. Lavelle. 2006. Soil macrofauna communities in Brazilian Amazonia. Pp. 43–55. *In* Soil Biodiversity in Amazonian and Other Brazilian Ecosystems. (F.M.S. Moreira, J.O. Siqueira & L. Brussaard, eds.). CAB International Publishing, Wallingford, UK.
- Barros, E., A. Neves, E. Blanchart, E.C.M. Fernandes, E. Wandelli & P. Lavelle. 2003. Development of the soil macrofauna community under silvopastoral and agrosilvicultural systems in Amazonia. *Pedobiologia* 47:273–280.
- Bornebusch, C.H. 1930. The Fauna of Forest Soil. Nielsen and Lydiche, Copenhagen. 224 pp.
- Breymeyer, A. 1967. Correlations between dry weight of spiders and their length and fresh weight. *Bulletin de l'Académie Polonaise des Sciences* 15:263–265.
- Brown, G.G., J. Römbke, H. Höfer, M. Verhaagh, K.D. Sautter & D.L.Q. Santana. 2006. Biodiversity and function of soil animals in Brazilian agroforestry systems. Pp. 217–242. *In* Sistemas Agroflorestais: Bases científicas para o desenvolvimento sustentado. (A.C. Gama-Rodrigues, E.F. Gama-Rodrigues, M.S. Viana, M.S. Freitas, J.M. Marciano, J.M. Jasmin, N.F. Barros & J.G.A. Carneiro, eds.). UENF, Campos dos Goytacazes, Rio de Janeiro.
- Chen, B. & D.H. Wise. 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology* 80:761–772.
- Clausen, I.H.S. 1983. Weight-length relations of eight species of spiders (Araneae) from Denmark. *Entomologiske Meddelelser* 50:139–144.
- Edwards, C.A. 1966. Relationships between weights, volumes and numbers of soil animals. Colloquium on Dynamics of Soil Communities, 5–10 September 1966, Braunschweig-Völkenrode. Friedr. Vieweg & Sohn GmbH, Braunschweig.
- Edwards, R.L. 1996. Estimating live spider weight using preserved specimens. *Journal of Arachnology* 24:161–166.
- Edwards, R.L. & W.L. Gabriel. 1998. Dry weight of fresh and preserved spiders (Araneida: Labidognatha). *Entomological News* 109:66–74.
- Hanagarth, W., H. Höfer, C. Martius, M.V.B. Garcia & J. Römbke. 2004. Soil fauna densities and fluctuations in central Amazonian forests and polycultures as affected by the El Niño and La Niña events in the years 1997–1999. *Environtopica* 1:1–18.
- Henschel, J.R., D. Mahsberg & H. Stumpf. 1996a. Mass-length relationships of spiders and harvestmen (Araneae and Opiliones). *In* Proceedings of the XIIIth International Congress of Arachnology, Geneve, September 1995. (V. Mahnert, ed.). *Revue Suisse de Zoologie*, vol. hors série 1:265–268.
- Henschel, J.R., H. Stumpf & D. Mahsberg. 1996b. Increase of arachnid abundance and biomass of water shores. *In* Proceedings of the XIIIth International Congress of Arachnology, Geneve, September 1995. (V. Mahnert, ed.). *Revue Suisse de Zoologie*, vol. hors série 1:269–278.

- Höfer, H. & A.D. Brescovit. 2001. Species and guild structure of a Neotropical spider assemblage (Araneae; Reserva Ducke, Amazonas, Brazil). *Andrias* 15:99–120.
- Höfer, H., W. Hanagarth, M.V.B. Garcia, C. Martius, E.N. Franklin, J. Römke & L. Beck. 2001. Structure and function of soil fauna communities in Amazonian anthropogenic and natural ecosystems. *European Journal of Soil Biology* 37:229–235.
- Jocqué, R. 1981. Size and weight variations in spiders and their ecological significance. *Biologisch Jaarboek* 49:155–165.
- Lang, A., S. Krooss & H. Stumpf. 1997. Mass-length relationships of epigeal arthropod predators in arable land (Araneae, Chilopoda, Coleoptera). *Pedobiologia* 41:327–333.
- Lavelle, P., E. Barros, E. Blanchart, G.G. Brown, T. Desjardins, L. Mariani & J.-P. Rossi. 2001. SOM management in the tropics: Why feeding the soil macrofauna? Pp. 53–62. *In* Managing Organic Matter in Tropical Soils: Scope and Limitations. (C. Martius, H. Tiessen & P.L.G. Vlek, eds.). Kluwer Academic Publishers, Dordrecht, Netherlands.
- Lavelle, P., D. Bignell, M. Lepage, V. Wolters, P. Roger, P. Ineson, O.W. Heal & S. Dhillon. 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. *European Journal of Soil Biology* 33:159–193.
- Lawrence, K.L. & D.H. Wise. 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. *Pedobiologia* 44:33–39.
- Lawrence, K.L. & D.H. Wise. 2004. Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia* 48:149–157.
- Martius, C., H. Höfer, M.V.B. Garcia, J. Römke & W. Hanagarth. 2004. Litter fall, litter stocks and decomposition rates in rain forest and agroforestry sites in central Amazonia. *Nutrient Cycling in Agroecosystems* 68:137–154.
- Mathieu, J., J.-P. Rossi, M. Grimaldi, P. Mora, P. Lavelle & C. Rouland. 2004. A multi-scale study of soil macrofauna biodiversity in Amazonian pastures. *Biology and Fertility of Soils* 40:300–305.
- Norberg, R.A. 1978. Energy content of some spiders and insects on branches of spruce (*Picea abies*) in winter; prey of certain passerine birds. *Oikos* 31:222–229.
- Rogers, L.E., R.L. Buschbom & C.R. Watson. 1977. Length-weight relationships of shrub-steppe invertebrates. *Annals of the Entomological Society of America* 70:51–53.
- Rogers, L.E., W.T. Hinds & R.L. Buschbom. 1976. A general weight vs. length relationship for insects. *Annals of the Entomological Society of America* 69:387–389.
- Sample, B.E., R.J. Cooper, R.D. Greer & R.C. Whitmore. 1993. Estimation of insect biomass by length and width. *American Midland Naturalist* 129:234–241.
- Schmidt, P., K. Dickow, A.A. Rocha, R. Marques, L. Scheuermann, J. Römke, B. Förster & H. Höfer. 2008. Soil macrofauna and decomposition rates in Southern Brazilian Atlantic rainforests. *Ecotropica* 14:89–100.
- Schoener, T.W. 1980. Length-weight regressions in tropical and temperate forest-understory insects. *Annals of the Entomological Society of America* 73:106–109.
- SPSS. 2002. SigmaPlot® 8.0.2. SPSS Inc, Chicago.
- StatSoft. 2005. Statistica 7.1. StatSoft, Inc, Tulsa, Oklahoma.
- Wise, D.H. 2004. Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. *Pedobiologia* 48:181–188.
- Wise, D.H., W.E. Snyder, P. Tuntibunpakul & J. Halaj. 1999. Spiders in decomposition food webs of agroecosystems: theory and evidence. *Journal of Arachnology* 27:363–370.

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Two new species of the spider genus *Ochyrocera* (Araneae, Ochyroceratidae) from Mexico

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Abstract. Two new species of the spider genus *Ochyrocera* Simon 1891 are described from Mexico. *Ochyrocera juquila* new species was collected under moist rotten logs and hollow trunks on a thick bed of pine needles in oak-pine forests located in a mountain range south of the city of Oaxaca at 1400–2700 m elev. *Ochyrocera juquila* resembles *O. quinquevittata* Simon 1891 from the Island of St. Vincent, in the angular shape of the embolus, which in the new species is V-shaped and in *O. quinquevittata* is L-shaped. *Ochyrocera chiapas* new species, was collected under rotten trunks and hollow trunks in abundant leaf litter in the tropical, humid Lacandona rainforest region located in eastern Chiapas, near the border with Guatemala. The species occurs at 160–260 m elev. *Ochyrocera chiapas* resembles *O. arietina* Simon, 1891 from the island of St. Vincent, in the similar shape of the embolus and distal apophysis of the embium, but in *O. chiapas* the embolus is more strongly curved and directed toward the distal part of the tibiae forming a “D”; in *O. arietina* the embolus is not as strongly curved as in *O. chiapas*. In both species, males and females were collected near each other; the females carried their egg sacs with their chelicerae. A key to the four known Mexican species is provided.

Resumen. Dos nuevas especies del género de arañas *Ochyrocera* Simon 1891 son descritas para México. *Ochyrocera juquila* nueva especie, fue colectada bajo troncos podridos y troncos huecos en una capa gruesa de agujas de pino, en bosque de pino-encino, en un sistema montañoso al sur de la ciudad de Oaxaca entre 1400–2700 m elev. *Ochyrocera juquila* está relacionada con *Ochyrocera quinquevittata* Simon 1891 de la Isla de San Vicente, en la forma angular del émbolo, el cual en la nueva especie es en forma de “V”, y en *O. quinquevittata* en forma de “L”. *Ochyrocera chiapas* nueva especie, fue colectada en bosque tropical, bajo troncos podridos y en troncos huecos con mucha humedad, y abundante hojarasca, en la región de la selva Lacandona localizada al este de Chiapas, cerca de la frontera con Guatemala, localizada entre 160–260 m elev. *Ochyrocera chiapas* está relacionada con *Ochyrocera arietina* Simon, 1891 de la Isla de San Vicente, en la forma similar del émbolo y apófisis distal del cimbio, pero en *O. chiapas* el émbolo es más fuertemente recurvado y dirigido hacia parte distal de la tibia formando una “D”, en *O. arietina* el émbolo no está fuertemente recurvado como en *O. chiapas*. En ambas especies, machos y hembras fueron coleccionados cercanamente entre ellos; las hembras cargaban sus sacos de huevos con los queliceros. Se presenta una clave de identificación para las cuatro especies mexicanas.

Keywords: Haplogynae, taxonomy, Oaxaca, Chiapas

The spider family Ochyroceratidae Fage 1912 has 14 genera and 155 species (Platnick 2008). Edwards et al. (2003) reported four genera from the western hemisphere: *Fageicera* Dumitrescu & Georgescu 1992 and *Speocera* Berland 1914, recorded only from Cuba, *Ochyrocera* Simon 1891 in the Caribbean region and Brazil, and *Theotima* Simon 1893 restricted to the Caribbean region.

Ochyroceratids are lucifugous spiders which live in leaf litter and detritus in mesic habitats, and many occur in caves as troglophiles (Gertsch 1973, 1977; Brignoli 1973; Lopez & Lopez 1997; Hormiga et al. 2007). These spiders spin tiny tangled webs in wall crevices and under litter (Gertsch 1973). *Ochyrocera* species build small, rather flimsy sheet webs with silk lines extending above the sheet that appear to serve as structural lines overlaid with finer silk lines running parallel to each other. The sheet is probably made of silk from the linearly arranged brush of posterior lateral spinneret aciniform gland spigots (Hormiga et al. 2007). There is limited published information available on the life history of these spiders (Edwards et al. 2003; Hormiga et al. 2007); some species of the family are parthenogenetic (Edwards et al. 2003).

Simon (1893) included *Theotima* and *Ochyrocera* in the Leptonetidae, where they remained until Fage (1912) erected the family Ochyroceratidae (Paquin & Ubick 2005). The genus *Ochyrocera* has 22 species, mostly from the Neotropical region (Brignoli 1974, 1978; Hormiga et al. 2007; Platnick 2008). In

the New World, the genus is found in Florida, Central America, and parts of South America. Some species are distributed in the West Indies, like Puerto Rico, where two undescribed, sympatric species of *Ochyrocera* occur in forest leaf litter (Simon 1891; Edwards et al. 2003; Paquin & Ubick 2005; Platnick 2008). Recently Hormiga et al. (2007) described *Ochyrocera cachote* from Hispaniola. Two species have been recorded from Mexico: *Ochyrocera fagei* Brignoli 1974 from Teopisca, Chiapas and *O. simoni* O. Pickard-Cambridge 1894 from Teapa, Tabasco. The objective of this contribution is to describe two new species recently collected in Mexico. *Ochyrocera juquila* new species and *O. chiapas* new species are the third and fourth species of the genus *Ochyrocera* from Mexico.

METHODS

The specimens, preserved in 80% ethanol, were examined with a Nikon SMZ645 stereoscope. A Nikon Coolpix S10 VR camera was used to photograph the dorsal view of the prosoma and opisthosoma of male and female specimens, and the internal genital area of females. The photographs were edited in Adobe Photoshop 7.0 to make the illustrations. The specimens were then processed in order that photomicrographs could be taken with an HITACHI S-2460N scanning electron microscope (SEM). All measurements of the descriptions are recorded in millimeters and SEM photomicrographs

are noted in microns. The map was done using Microsoft Encarta Encyclopedia and was edited in Adobe Photoshop 7.0. The specimens are deposited in the Colección Nacional de Arácnidos (CNAN) of the Instituto de Biología, Universidad Nacional Autónoma de México, México D. F. (IBUNAM) and the American Museum of Natural History (AMNH), New York, USA. Abbreviations used in the description are: ALE, anterior lateral eyes; ALS, anterior lateral spinnerets; AME, anterior median eyes; B, bulb of the palp; C, cymbium; DAC, distal apophysis of cymbium; E, embolus; PLE, posterior lateral eyes; PLS, posterior lateral spinnerets; PMS, posterior median spinnerets; S, spermathecae.

TAXONOMY

Family Ochyroceratidae Fage 1912

Genus *Ochyrocera* Simon 1891

Type species.—*Ochyrocera arietina* Simon 1891

Ochyrocera juquila new species

Figs. 1–10

Type material.—MEXICO: *Oaxaca*: 1 ♂ holotype (CNAN-T0314), 5 km from Juquila to Panixtlahuaca, Municipio Santa Catarina Juquila (16°15.071'N, 97°18.799'W, 1447 m), 27 June 2006 (A. Valdez, O. Francke, H. Montaña, G. Villegas, C. Santibañez, cols.). Paratypes: 1 ♀ with egg sac (CNAN-T0315), 4 ♀♀ (2 with egg sac), 1 ♂, 1 ♂ subadult (CNAN-T0319) and 1 ♀, 1 ♂ (AMNH), same data as holotype; 1 ♂ (CNAN-T0316), turn off to Magdalena Mixtepec, Municipio Magdalena Mixtepec (16°55.811'N, 96°52.455'W, 2676 m), 3 December 2005 (A. Valdez, O. Francke, H. Montaña, cols.); 4 ♀♀, 1 ♂ (CNAN-T0317), 3 km E of turn off to Santa Inés del Monte, Municipio Santa Inés del Monte (16°56.445'N, 96°51.631'W, 2665 m), 3 December 2005 (A. Valdez, O. Francke, H. Montaña, cols.); 1 ♀ (CNAN-T0318), 10 km S of San Jerónimo Coatlán, Municipio San Jerónimo Coatlán (16°12.917'N, 96°54.206'W, 2160 m), 25 June 2006 (A. Valdez, O. Francke, H. Montaña, G. Villegas, C. Santibañez, cols.); 9 ♀♀ (5 with egg sac), 1 ♂ (CNAN-T0320), 10 km SW of San Pablo Coatlán, Municipio San Pablo Coatlán (16°11.343'N, 96°48.687'W, 1855 m), 25 June 2006 (A. Valdez, O. Francke, H. Montaña, G. Villegas, C. Santibañez, cols.).

Etymology.—The specific name is a noun in apposition and refers to the municipality of the type locality: Santa Catarina Juquila, Oaxaca, Mexico.

Diagnosis.—Males can be distinguished by the embolus bent over 75° with a basal protuberance near the bulb, the globular bulb, and the cymbial apophysis with hook-shaped tip (Figs. 3, 4). Females can be distinguished by the oval genital area with two parts, the anterior one larger than the posterior part (Fig. 9).

Description.—Male (holotype): Specimen preserved in alcohol with carapace fuchsia, fovea indistinct (Fig. 1). Clypeus long, same color as carapace. Chelicerae pale yellow, fangs light orange with seven small teeth and one large tooth on a single line (Fig. 2). Six eyes in three groups, slightly elevated with black rings around them (Fig. 1). Sternum circular, wider than long; light violet with faint dark stripes. Labium longer than wide, not fused to the sternum. Endites pale yellow, longer than wide, convergent, with small violet

spots. Coxae fuchsia. Trochanters and patellae pale yellow. Legs fuchsia. Distal part of femora pale yellow. Patellae pale yellow. Proximal and distal parts of metatarsus and tarsus pale yellow. Metatarsus and tarsus with pseudosegmentation. Opisthosoma oval, dark gray (Fig. 1). Ventral plate of gonopore violet. ALS conical, PMS slender and longer than ALS, PLS cylindrical and stout. Spinnerets pale violet.

Palp: Tibia long and cylindrical (Figs. 3, 4), pale fuchsia; distal apophysis of cymbium hooked (Figs. 3, 4). Bulb globular, with a basal protuberance (Figs. 3, 4). Embolus long, V-shaped, with distal part curved and sclerotized (Figs. 3–6).

Measurements: Total length 1.23. Carapace 0.52 long, 0.47 wide. Clypeus length 0.09. Diameter of AME 0.04, ALE 0.05, PLE 0.06. Sternum 0.36 long, 0.34 wide. Leg lengths: I- femur 1.07/ patella 0.17/ tibia 1.25/ metatarsus 0.84/ tarsus 0.59/ total 3.92; II- 0.92/ 0.18/ 1.0/ 0.68/ 0.53/ 3.31; III- 0.71/ 0.16/ 0.81/ 0.60/ 0.45/ 2.73; IV- 0.98/ 0.18/ 1.16/ 0.75/ 0.59/ 3.66. Leg formula: 1-4-2-3.

Female (Paratype): Differs from male as follows: carapace violet. Clypeus high (Fig. 7), same color as carapace. Chelicerae fuchsia on frontal face and light yellow on prolateral face (Fig. 8). Fangs orange. Sternum circular, violet without stripes. Opisthosoma larger than in the male.

Genital area: Poorly chitinized, oval with two parts in ventral view, anterior part larger than posterior (Fig. 9). Spermathecae oval and separated, with visible long and thin prolongations toward posterior part of genital area (Fig. 10).

Measurements: Total length 1.26. Carapace 0.58 long, 0.49 wide. Clypeus length 0.08. Diameter of AME 0.04, ALE 0.04, PLE 0.05. Sternum 0.36 long, 0.34 wide. Leg lengths: I- femur 0.9/ patella 0.18/ tibia 1.04/ metatarsus 0.68/ tarsus 0.46/ total 3.26; II- 0.74/ 0.17/ 0.82/ 0.58/ 0.46/ 2.77; III- 0.65/ 0.16/ 0.69/ 0.52/ 0.42/ 2.44; IV- 0.88/ 0.13/ 0.97/ 0.66/ 0.51/ 3.15. Leg formula: 1-4-2-3.

Variation.—Total length: 1.2–1.4. Coloration: some specimens fuchsia, pale orange, or purple on the prosoma and the legs. The opisthosoma varies from light blue to dark gray.

Distribution.—Known only from the type localities (Fig. 20).

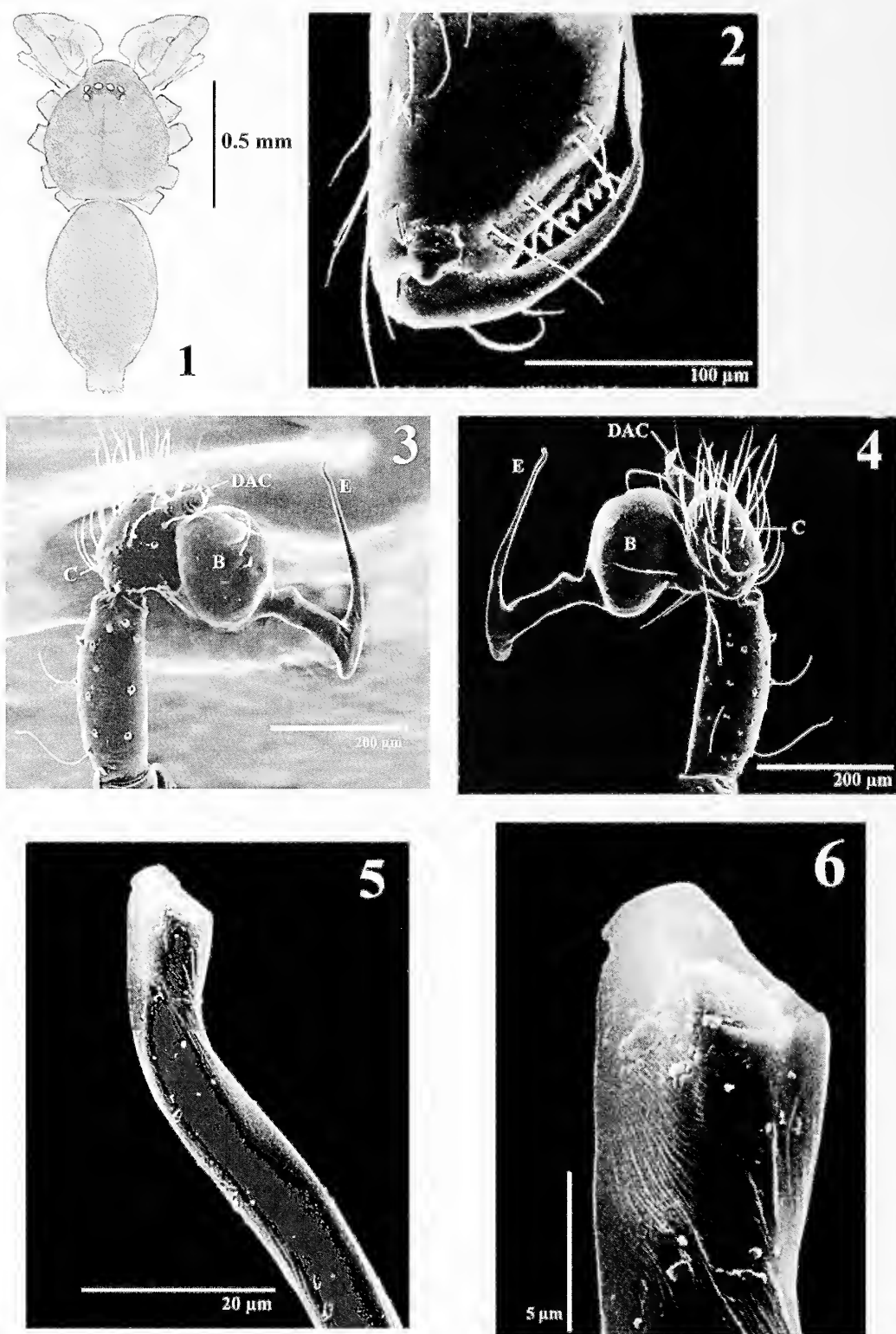
Related species.—*Ochyrocera juquila* resembles *O. quinquevittata* Simon 1891 from the Island of St. Vincent in the angular shape of the embolus, which in the new species is V-shaped (75°), and in *O. quinquevittata* is L-shaped. The distal apophysis of the cymbium of the palp with hook shape is curved and short in *O. juquila*, whereas in *O. quinquevittata* it is straight and long. Finally, the bulb in *O. juquila* is globular, whereas in *O. quinquevittata* it is oval.

Natural History.—The specimens of *Ochyrocera juquila* were collected under moist rotten logs and hollow trunks on a thick bed of pine needles in oak-pine forests located in a mountain range south of the city of Oaxaca at 1400–2700 m elev. Males and females were collected near each other, and the females carried their egg sacs with the chelicerae.

Ochyrocera chiapas new species

Figs. 11–19

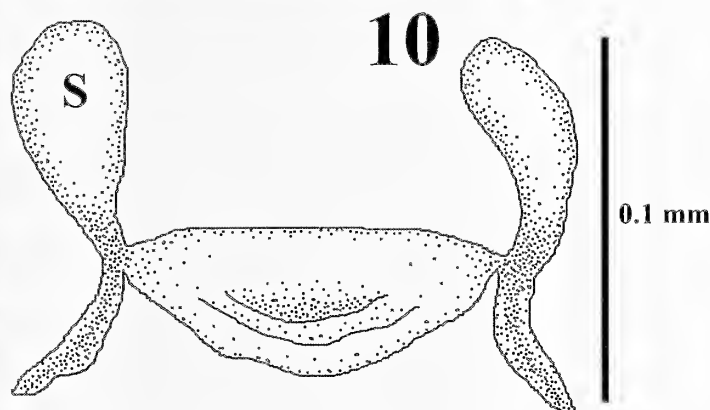
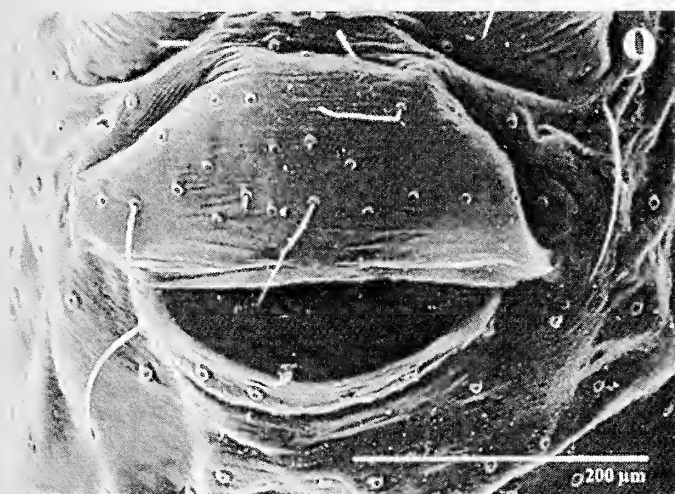
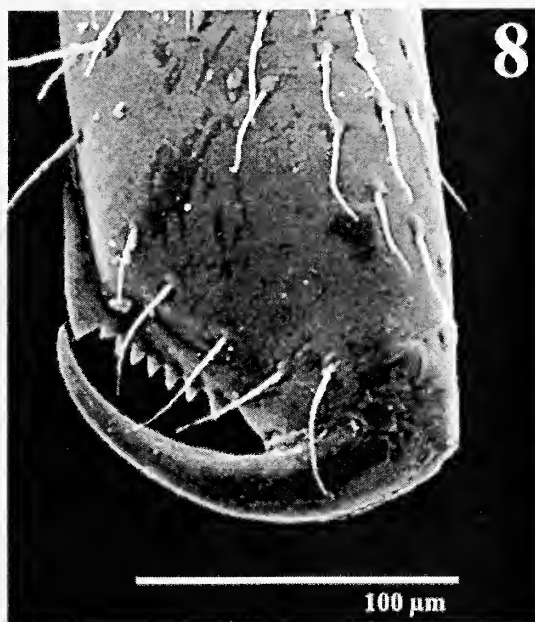
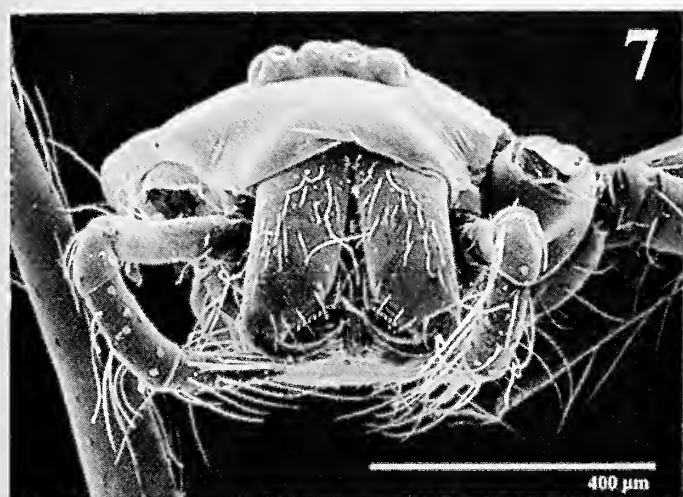
Type material.—MEXICO: *Chiapas*: 1 ♂ holotype (CNAN-T0321) from El Taller, Sierra de la Cojolita, Municipio Ocosingo (16°45.756'N, 91°01.933'W, 257 m), 9 August 2005



Figures 1–6.—*Ochyrocera juquila* new species, male: 1. Prosoma and opisthosoma, dorsal view; 2. Right chelicera, anterior view; 3. Left palp, prolateral view; 4. Left palp, retrolateral view; 5. Embolus; 6. Embolus, apical view.

(A. Valdez, G. Montiel, R. Paredes, E. Cabrera, A. Ávila, A. Ibarra, J. Castelo cols.). Paratypes: 1 ♀, 1 ♂ and 1 juvenile (CNAN-T0322), same data as holotype; 1 ♀, 1 juvenile (CNAN-T0323) from Reserva Comunal de la Cruz, km 150 marker on Crucero Corozal-Benemérito road, Municipio Ocosingo (16°42.878'N, 90°54.328'W, 167 m), 9 August

2006 (A. Valdez, H. Montaña, S. Rubio, N. Pérez, I. Mondragón, cols.); 1 ♀, and 3 juveniles (CNAN-T0327), same locality, 8 May 2006 (A. Valdez, H. Montaña, G. Montiel, R. Paredes, M. Guzmán, cols.); 4 ♀♀, 1 ♂ and 3 juveniles (CNAN-T0324) from Arroyo Nayte, Sierra de la Cojolita, Municipio Ocosingo (16°45.546' N, 91°02.629' W, 209 m), 18 October



Figures 7–10.—*Ochyrocera juquila* new species, female: 7. Carapace, anterior view; 8. Left chelicerae, anterior view; 9. Genital area, ventral view; 10. Genital area, dorsal view.

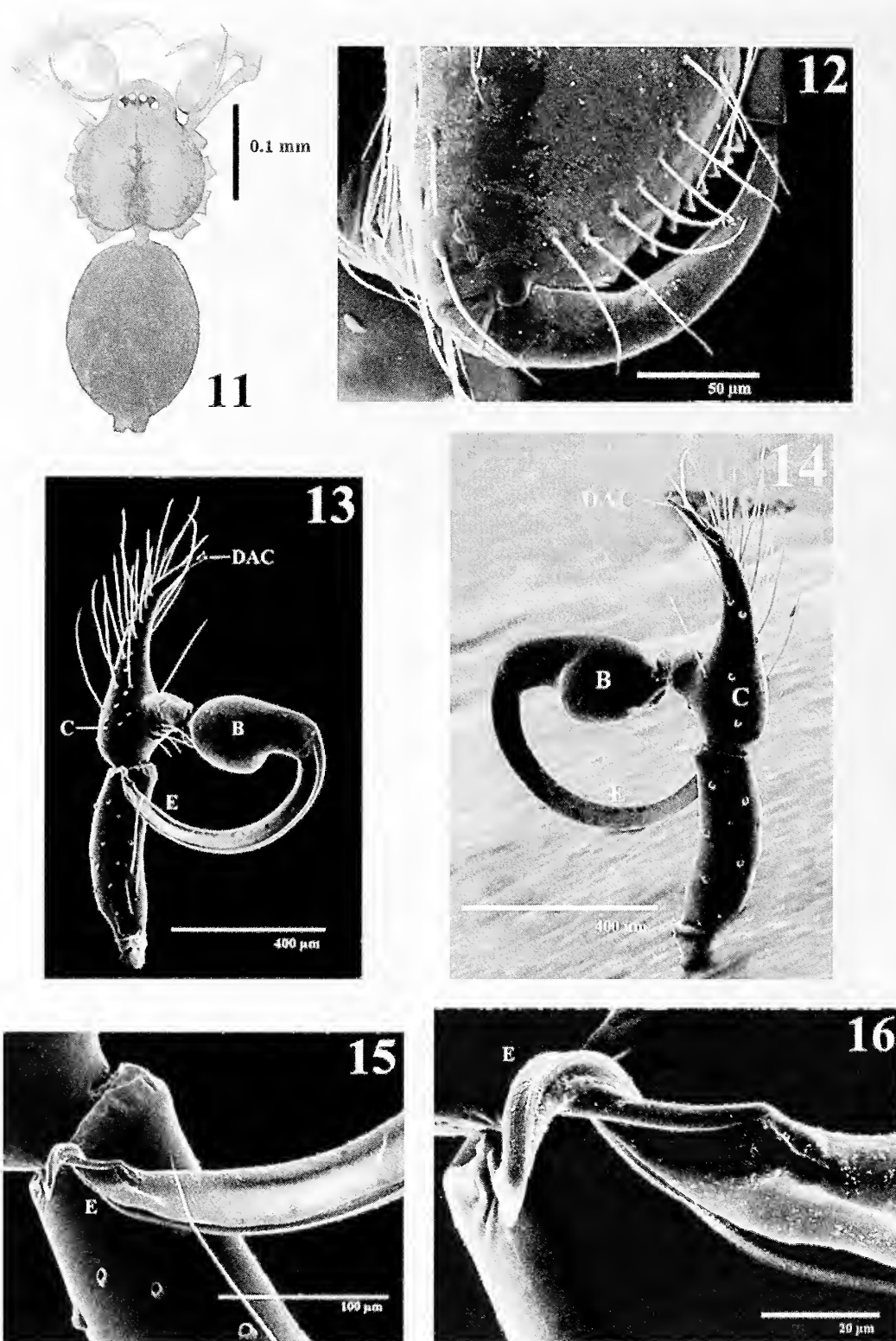
2006 (A. Valdez, O. Francke, H. Montaña, A. Ballesteros, cols.); 1 ♂ (CNAN-T0328), same locality, 9 August 2006 (A. Valdez, H. Montaña, S. Rubio, N. Pérez, I. Mondragón, cols.); 1 ♀ (CNAN-T0330), same locality, 3 October 2005 (H. Montaña, G. Montiel, I. Mondragón, cols.); 1 ♀ (CNAN-T0325) from El Aserradero, Municipio Ocosingo (16°47.119'N, 91°02.290'W, 205 m), 6 September 2005 (A. Valdez, O. Francke, H. Montaña, A. Jaimes, M. Córdova, cols.); 1 ♂ (AMNH), same locality, 18 October 2006 (A. Valdez, O. Francke, H. Montaña, A. Ballesteros, cols.); 2 ♀♀, 4 juveniles (CNAN-T0326), same locality, 18 October 2006 (A. Valdez, O. Francke, H. Montaña, A. Ballesteros, cols.); 2 ♀♀, 2 ♂♂, 3 ♂♂ subadult (CNAN-T0329) from El Encaño, Sierra de la Cojolita, Municipio Ocosingo (16°48.677' N, 91°04.646' W, 165 m), 3 October 2005 (H. Montaña, G. Montiel, I. Mondragón, cols.); 2 ♀♀ (AMNH), same locality, 3 October 2005 (H. Montaña, G. Montiel, I. Mondragón, cols.).

Etymology.—The specific name is a noun in apposition and refers to the state of the type locality: Chiapas, Mexico.

Diagnosis.—Males can be distinguished by the D-shaped embolus directed toward the distal part of the tibia, and the

conical shape of the distal cymbial apophysis, curved distally with one terminal claw (Figs. 13, 14). Females can be distinguished by the mouth-like form of the genital area (Fig. 18).

Description.—Male (holotype): Specimen preserved in alcohol with carapace dark blue with darker regions around the fovea, and on the lateral margins (Fig. 11). Clypeus long, same color as carapace. Chelicerae blue-green, with seven small teeth and one large tooth on a single line (Fig. 12). Fangs dark orange. Six eyes in three groups, slightly elevated, with black rings around them. Sternum dark blue, with a white central spot, wider than long. Labium square, as wide as long, dark blue, not fused to the sternum. Endites green, convergent, longer than wide. Coxae greenish, darker distally. Trochanters greenish. Femur I yellowish. Femora II–IV pale fuchsia, bluish distally. Patellae pale. Tibiae, metatarsi and tarsi yellowish. Opisthosoma oval, longer than wide and deep, dark blue (Fig. 11). Ventral plate of gonopore pale blue. ALS cylindrical. PMS slender and smaller than the others. PLS conical. All spinnerets same color as opisthosoma.

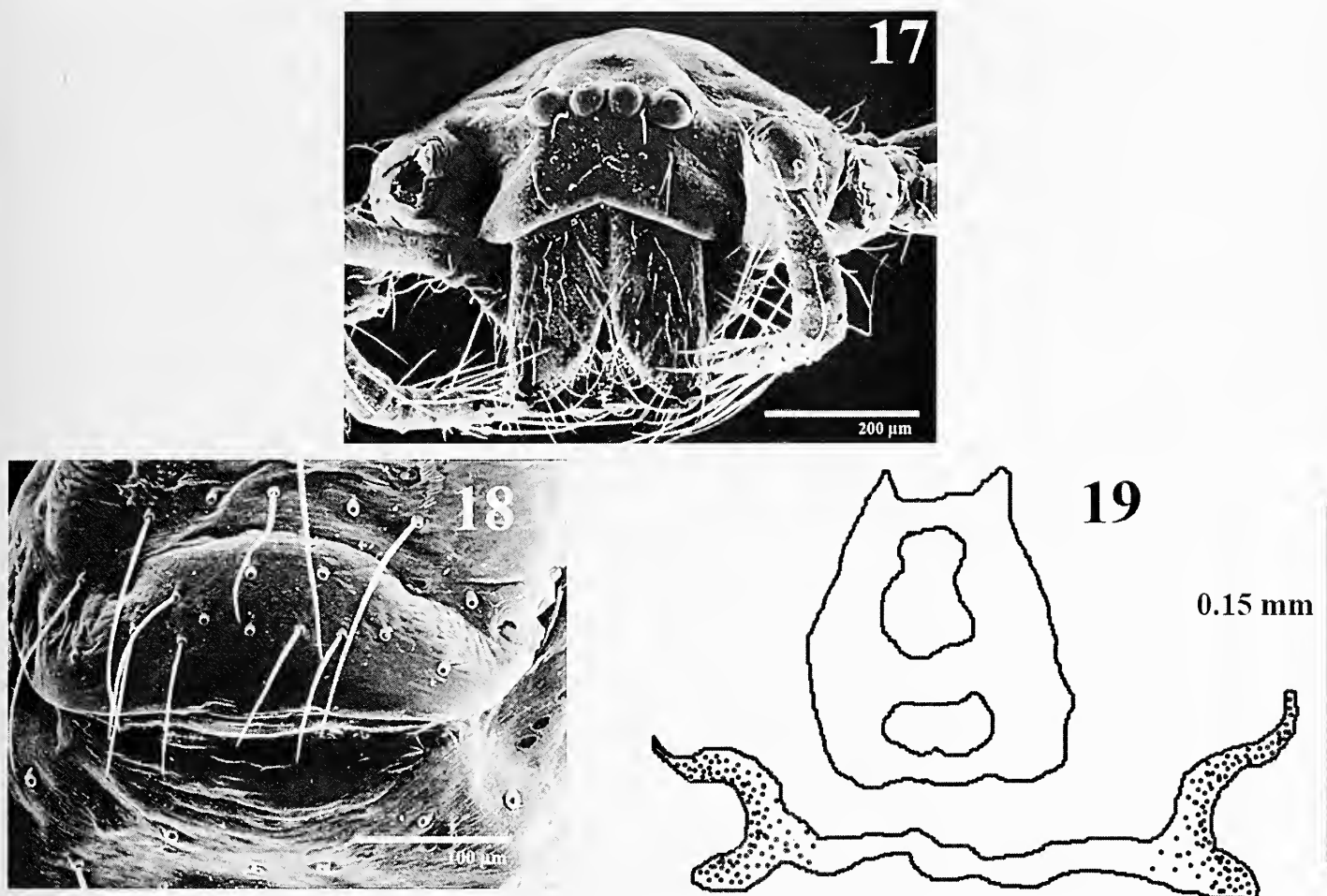


Figures 11–16.—*Ochyrocera chiapas* new species, male: 11. Prosoma and opisthosoma, dorsal view; 12. Right chelicera, anterior view; 13. Left palp, prolateral view; 14. Left palp, retrolateral view; 15. Embolus; 16. Embolus, apical view.

Palp: Tibia long and cylindrical, distal apophysis of cymbium conical, curved distally (Figs. 13, 14). Globular bulb; embolus long and curved with D-shape, in prolateral view directed towards distal part of the tibia (Fig. 13).

Embolus wider distally, with marked apical curvature with hook-shape (Figs. 15, 16).

Measurements: Total length 1.68. Carapace 0.78 long, 0.67 wide. Clypeus length 0.17. Diameter of AME 0.05, ALE 0.06,



Figures 17–19.—*Ochyrocera chiapas* new species, female: 17. Carapace, anterior view; 18. Genital area, ventral view; 14. Genital area, dorsal view.

PLE 0.04. Sternum 0.36 long, 0.48 wide. Leg lengths: I- femur 3.3/ patella 0.24/ tibia 3.7/ metatarsus 2.4/ tarsus 1.23/ total 10.87; II- 2.3/ 0.2/ 2.47/ 1.63/ 0.93/ 7.53; III- 1.75/ 0.2/ 1.74/ 1.23/ 0.77/ 5.69; IV- 2.3/ 0.23/ 2.52/ 1.58/ 1.03/ 7.66. Leg formula 1-4-2-3.

Female (Paratype): Differs from male as follows: fangs of chelicerae pale reddish, darker at base (Fig. 17). Endites dark blue, lighter basally. Coxae dark blue, lighter basally. Trochanters light blue with dark blue spots. Femora and tibiae purple, white distally. Patellae dark blue. Metatarsi and tarsi pale. Opisthosoma more voluminous than in male.

Genital area: Weakly sclerotized, light blue, mouth-shaped in ventral view (Fig. 18). Spermathecae slender and curved, separated by a visible duct (Fig. 19).

Measurements: Total length 1.76. Carapace 0.75 long, 0.65 wide. Clypeus length 0.18. Diameter of AME 0.04, ALE 0.06, PLE 0.04. Sternum 0.4 long, 0.44 wide. Leg lengths: I- femur 2.78/ patella 0.24/ tibia 3.1/ metatarsus 2.05/ tarsus 1.16/ total 9.33; II- 1.95/ 0.22/ 2.0/ 1.23/ 0.5/ 5.9; III- 1.54/ 0.2/ 1.6/ 1.16/ 0.75/ 5.25; IV- 2.06/ 0.21/ 2.15/ 1.46/ 0.93/ 6.81. Leg formula: 1-4-2-3.

Variation.—Total length: 1.6–1.75. Coloration: carapace varies from clear blue to greenish. Chelicerae ranges from blue-green to pale green. The white central spot of the sternum is small, circular in some specimens; in others longitudinal, wide or thin. Some specimens have legs fuchsia and others pale

fuchsia. Sternum and labium vary from dark blue to light blue. Endites and coxae greenish on males and on the females between dark and light blue.

Distribution.—Known only from the localities of the type material (Fig. 20).

Related species.—*Ochyrocera chiapas* resembles *O. arietina* Simon, 1891 from the island of St. Vincent, in the similar shape of the embolus and distal apophysis of cymbium, but in *O. chiapas* the embolus is more strongly curved and directed toward the distal part of the tibiae forming a “D;” in *O. arietina*, the embolus is not as strongly curved as in *O. chiapas*. In addition, in *O. arietina* the embolus is directed toward the distal apophysis of the cymbium and not toward the tibia like in *O. chiapas*. The distal apophysis of the cymbium of the palp in *O. chiapas* has a claw-shaped curve and an index-finger shape in *O. arietina*; finally the tibia of the palp in *O. chiapas* is longer and cylindrical, whereas in *O. arietina* it is shorter and oval.

Natural History.—The specimens of *O. chiapas* were collected at an elevation between 160–260 m in high humidity under rotten logs, hollow trunks, and abundant leaf litter. The habitat was in tropical rainforest, in the Lacandona region located in eastern Chiapas, near the border with Guatemala. Males and females were collected near each other, and the females carried their egg sacs with the chelicerae.

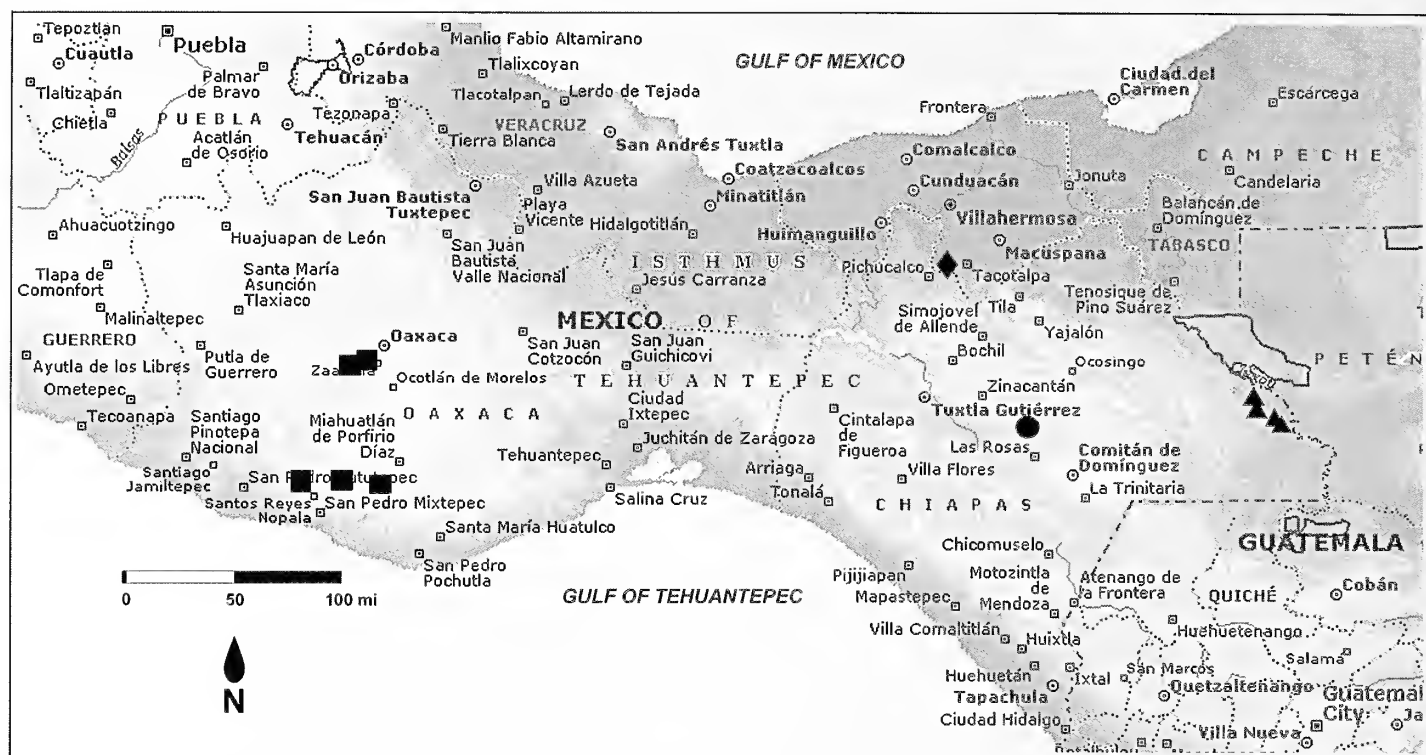


Figure 20.—Distribution records of *Ochyrocera* from Mexico: *O. juquila* new species (■), *O. chiapas* new species (▲), *O. simoni* O. Pickard-Cambridge 1894 (◆), and *O. fagei* Brignoli 1974 (●).

KEY TO SPECIES OF *ochyrocer* FROM MEXICO:

1. Distal apophysis on cymbium claw-shaped; bulb of the palp oval (Figs. 13, 14) 2
 Distal apophysis of cymbium other form; bulb of the palp globular (Figs. 3, 4) 3
2. Embolus slender and long, D-shaped, directed toward the distal part of the tibia (Figs. 13, 14) *O. chiapas* new species.
 Embolus stout and short, V-shaped, directed toward the centre of the cymbial apophysis *O. fagei* Brignoli 1974.
3. Embolus slender in distal part and stout in basal part, V-shaped, with a basal protuberance; cymbial apophysis with hooked tip (Figs. 3, 4) *O. juquila* new species.
 Embolus slender and long, J-shaped; distal cymbial apophysis wider in the centre; tibia of the palp wider at tip *O. simoni* O. Pickard-Cambridge 1894.

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infinite help with fieldwork. The specimens were collected under Scientific Collector Permit FAUT-0175 from the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT), to Dr. Oscar F. Francke.

LITERATURE CITED

- Brignoli, P.M. 1973. Notes on spiders, mainly cave-dwelling, of Southern Mexico and Guatemala (Araneae). *Accademia Nazionale del Lincei* 171:195–238.
- Brignoli, P.M. 1974. Ragni del Brasile I. *Ochyrocera viridissima* n. sp. (Araneae, Ochyroceratidae). *Revue Suisse de Zoologie* 81:77–81.
- Brignoli, P.M. 1978. Spinnen aus Brasilien, II. Vier neue Ochyroceratidae aus Amazonas nebst Bemerkungen über andere Amerikanische Arten (Arachnida: Araneae). *Studies on Neotropical Fauna and Environment* 13:11–21.
- Edwards, R.L., E.H. Edwards & A.D. Edwards. 2003. Observations of *Theotima minutissimus* (Araneae, Ochyroceratidae), a parthenogenetic spider. *Journal of Arachnology* 31:274–277.
- Fage, L. 1912. Etudes sur les araignées cavernicoles. I. Revision des Ochyroceratidae (n. fam.). In *Biospélogica*, XXV. Archives de Zoologie Experimentale et Generale (5) 10:97–162.

- Gertsch, W.J. 1973. A report on cave spiders from Mexico and Central America. *Bulletin of Association for Mexican Cave Studies* 5:141–163.
- Gertsch, W.J. 1977. Report on cavernicole and epigean spiders from the Yucatan Peninsula. *Bulletin of Association for Mexican Cave Studies* 6:103–131.
- Hormiga, G., F. Álvarez-Padilla & S.P. Benjamin. 2007. First records of Extant Hispaniolan spiders of the families Mysmenidae, Symphytognathidae, and Ochyroceratidae (Araneae), including a new species of *Ochyrocera*. *American Museum Novitates* 3577:1–21.
- Lopez, A. & B. Lopez. 1997. Observations sur deux araignées de la Grotte Fourgassie (Guyana Française): *Paratropis papilligera* Pick. Cambr., 1896 (Mygalomorphae: Paratropididae) et *Ochyrocera caeruleoamethystina* n. sp. (Araneomorphae: Ochyroceratidae). *Mémoires de Biospéologie* 24:33–42.
- Paquin, P. & D. Ubick. 2005. Ochyroceratidae. P. 181. *In* *Spiders of North America: an Identification Manual*. (D. Ubick, P. Paquin, P.E. Cushing & V. Roth, eds.). American Arachnological Society, Keene, NH.
- Platnick, N.I. 2008. The World Spider Catalog, Version 8.1. American Museum of Natural History, New York. Online at <http://research.amnh.org/entomology/spiders/catalog/index.html>
- Simon, E. 1891. On the spiders of the island of St. Vincent. Part 1. *Proceedings of the Zoological Society of London* 1891:549–575.
- Simon, E. 1893. *Histoire naturelle des Araignées*. Tome 1, Fascicule II. Seconde édition. Paris, Librairie encyclopédique de Roret. 256 pages.

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Two new species of the genus *Diplothele* (Araneae, Barychelidae) from Orissa, India with notes on *D. walshi*

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Abstract. The genus *Diplothele* O. Pickard-Cambridge 1890 of the brush-footed spider family Barychelidae is represented in India by a single species, *D. walshi* O. Pickard-Cambridge 1890. In this paper, we describe two new species: *Diplothele gravelyi* from Angul and *Diplothele tenebrosus* from Ganjam, Orissa. We establish a neotype and provide additional characters for *D. walshi*, the types of which are lost. The neotype was collected from one of the previously described localities, Barkuda Island, Orissa. Spiders of this genus are known to build double-door trapdoor burrows, but the new species, *D. tenebrosus*, constructs a single entrance burrow with a trapdoor. Notes on natural history are provided for all species.

Keywords: New species, neotype, taxonomy, spider

The brush-footed spider family Barychelidae is represented worldwide by 44 genera and 300 species, of which four genera and five species—*Diplothele walshi* O. Pickard-Cambridge 1890, *Sason andamanicum* Simon 1888, *Sason robustum* O. Pickard-Cambridge 1883, *Sasonichus sullivanii* Pocock 1900, and *Sipalolasma arilrapophys* Gravely 1915—are reported from India (Siliwal & Molur 2007; Platnick 2008).

The genus *Diplothele* O. Pickard-Cambridge 1890 is endemic to South Asia and is represented by two species, namely *Diplothele walshi* O. Pickard-Cambridge 1890 from India and *Diplothele halyi* Simon 1892 from Sri Lanka. The trapdoor spiders we collected recently from Angul and Ganjam districts in Orissa have only two spinnerets, which after we consulted the literature (O. Pickard-Cambridge 1890; Pocock 1900; Raven 1985) were recognized as *Diplothele* spp. The description of *D. walshi* provided by O. Pickard-Cambridge (1890) is elementary and is not very helpful in comparative taxonomic work, as it lacks information on spermathecal structure. Most morphological characters of the new material from Orissa matched O. Pickard-Cambridge's description of *D. walshi* except for size. Specimens from Angul and Ganjam were much larger than reported for *D. walshi*. Even Gravely (1921, 1935) emphasized that *D. walshi* were small spiders (less than 10 mm), and he reported that the specimens from Horsleykonda, Chittoor district, in the Madras Museum collection were suspected to be new species because the size of these spiders was almost double that of *D. walshi*. Also, burrow structure of the *Diplothele* sp. observed at Angul and Ganjam did not match that reported for *D. walshi* by Gravely (1921).

To resolve the confusion, it was necessary to re-collect *D. walshi* from known localities. The type locality of *D. walshi* is the state of Orissa (O. Pickard-Cambridge 1890; Pocock 1900); fortunately, Gravely (1921) had also reported this species from Barkuda Island, Chilika Lake, Orissa. Therefore, Barkuda Island was surveyed rapidly in August 2007 for trapdoor spiders, and a few mature female individuals of *Diplothele* sp.

were collected. These spiders were smaller, different in morphology as well as in habit, and matched the description of *D. walshi* (Gravely 1921). After examining the spermathecae of specimens from Barkuda Island and comparing them with those of specimens from Angul and Ganjam, it was clear that the latter were new species of *Diplothele*.

Unlike most of O. Pickard-Cambridge's type specimens preserved in the Hope Entomological Collection (OUMNH), Oxford, the holotype of *D. walshi* is currently missing (in litt., Zoe Simmons, Collections staff at OUMNH). Raven (1985) reported its absence and on a personal visit to the collection failed to locate the type. To further confirm its status, we inquired through major European museums, including NHM (London), about the type specimen of *D. walshi*, but could not locate it. It is confirmed now that the type specimen of *D. walshi* is lost. We therefore assign a *neotype* for this species from Barkuda Island, one of the confirmed localities of *D. walshi*.

In the present paper, we describe two new species: *Diplothele gravelyi* from the Angul district, and *D. tenebrosus* from the Ganjam district of Orissa, both based on mature females. We did a rapid survey and did not make a concerted effort to search for males. We also provide additional taxonomic details for *D. walshi* and notes on natural history for all the species. We compare important taxonomic characteristics for the three Indian species (Table 1).

METHODS

All specimens were deposited in the Wildlife Information Liaison Development Society, Coimbatore, Tamil Nadu, India. Measurements of body parts except for the eyes were taken with a MitutoyoTM Vernier Caliper. Eye measurements were made with a calibrated ocular micrometer. All measurements are in mm. Spermathecae were dissected and cleared in concentrated lactic acid in a 100° C water bath for 15–20 min. Total length excludes chelicerae. All illustrations were prepared with the help of a camera lucida attached to a CETIITM stereomicroscope by MS.

Table 1.—Taxonomic characteristics of three *Diplothele* species.

Character	<i>D. walshi</i>	<i>D. gravelyi</i>	<i>D. tenebrosus</i>
Size range of spider	7.42–10.60 mm	14.70–16.90 mm	17.00–21.62 mm
Color of spider in life	yellowish-brown	brown	dark brown
PMS	absent	absent	absent
No. of maxillary cuspules	absent	3–4	3
Dorsal pattern on abdomen	chevron	chevron	chevron
Ventral pattern on abdomen	mottled	few small dots	pallid
Rastellum	9 short spines	27–30 short spines	39–42 short spines
Promarginal teeth (basomesal teeth)	7(12)	8(24)	9(20)
Patellae thorns III(IV)	present (absent)	present (absent)	absent (absent)
scopula metatarsi III(IV)	1/4(few scopuliform hair distally)	1/4(few scopuliform hair distally)	1/2(1/4)
Mt preening combs III(IV)	present	present	present
Shape of stalk of female spermathecae	digitiform	digitiform	broader at base and gradually narrowing towards apex
Shape of outer lobes of female spermathecae	lobe with sclerotized and twisted stalk	curved towards inner side with constriction at base and a notch towards distal end	balloon shape with constriction at base
Habitat	sandy soil, below shrubs, between roots	rocky, close to water body, dry deciduous forest	roadside, mango orchard with dense undergrowth
No. of burrow entrances (distance between the two entrances)	two (diameter of entrance)	two (two times entrance diameter)	one
Shape of burrow	flimsy short fork/'Y' shape	perfect fork/'Y' shape	bulb like
Distribution	Barkuda Island and nearby areas in Balugaon and Ganjam, Orissa	Satkosia WLS and nearby areas in Angul district, Orissa	Jadeshwar, Huma in Ganjam district; Berbera in Puri district, Orissa

Abbreviations.—ALE = anterior lateral eye, AME = anterior median eye, MOQ = median ocular quadrate, MS = Manju Siliwal, Neo = Neotype, NHM = Natural History Museum, PLE = posterior lateral eye, OUMNH = Oxford University Museum of Natural History, PME = posterior median eye, PLS = posterior lateral spinnerets, PMS = posterior median spinnerets, STC = Superior or paired tarsal claws, WILD = Wildlife Information Liaison Development Society. Abbreviations used for hair and spines count are d = dorsal, fe = femur, mt = metatarsus, p = prolateral, pa = patella, r = retrolateral, ta = tarsus, ti = tibia, v = ventral.

TAXONOMY

Diplothele O. Pickard-Cambridge 1890

Diplothele O. Pickard-Cambridge 1890:621; Simon 1892:123; Pocock 1900:174–175; Raven 1985:114, 145.

Adelonychia Walsh 1891:269; Gravely 1915:263; Raven 1985:145. First synonymized by Gravely (1915) and holotype considered lost by Raven (1985).

Type species.—*Diplothele walshi* O. Pickard-Cambridge 1890 is based on single female specimen. The holotype is lost; it was deposited at Hope Entomological Collections, Oxford University Museum of Natural History, Oxford, where most of the O. Pickard-Cambridge spider collection is deposited, and collection records in 1985 (I. Lansbury, in litt.) confirmed the type should be held by OUMNH.

The holotype female of *Adelonychia nigrostriata* Walsh 1891 from Khurda, Orissa state, India, is also lost. Since the species is considered synonymous with *D. walshi*, it does not constitute a nomenclatural problem requiring a neotype.

Diagnosis.—Two spinnerets. Anterior lateral eyes on clypeal edge, separated by less than their diameter, AME close to each other; ocular group wider behind than in front. Rastellum on low mound consisting of long, thick, curved, randomly arranged spines. Labium without cuspules, wider than long. Maxillae with few cuspules in anterior corner. Legs short, stout, anterior pair without spines; scopulae on metatarsi I–II and tarsi I–IV present, metatarsi III–IV weakly scopulated; STC of legs I and II clearly smaller than on legs III and IV (O. Pickard-Cambridge 1890, Pocock 1900, Raven 1985). Bilobed spermathecae.

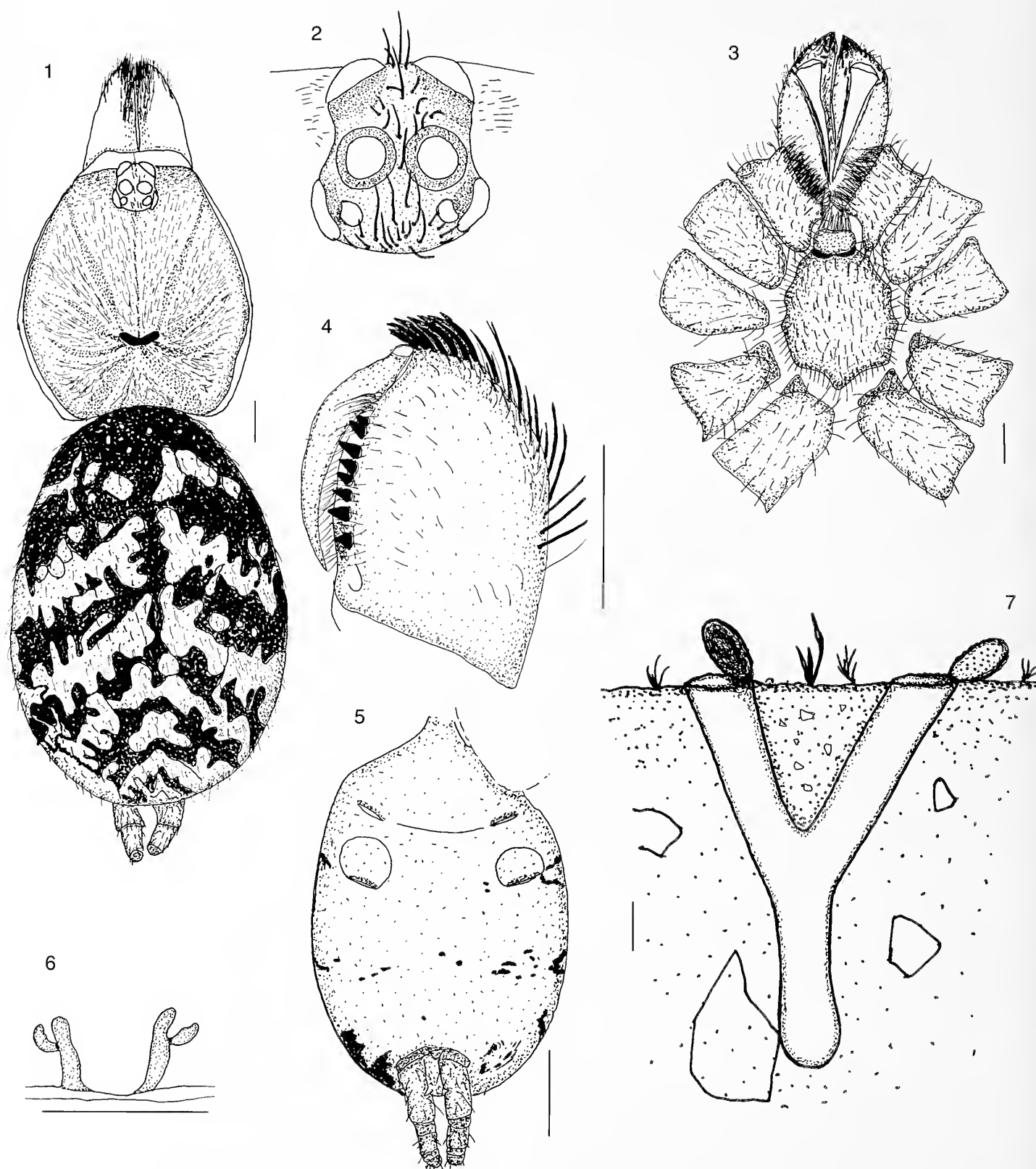
Distribution.—Endemic to India and Sri Lanka.

Diplothele gravelyi new species

Figs. 1–7

Type specimens.—INDIA: Orissa: holotype female, near Satkosia Wildlife Sanctuary, Angul district, 93 m elev., 20°51'N, 84°91'E, 3 April 2007, M. Siliwal, S. Behera (WILD-07-ARA-161); 1 paratype female, same data as holotype (WILD-07-ARA-162).

Diagnosis (female).—The new species *Diplothele gravelyi* differs from *D. halyi* and resembles *D. walshi* in having the metatarsi longer than the tarsi of all legs. It differs from *D. walshi* in being about 1.5–2.2 times larger, having more rastellar spines, the presence of 3–4 cuspules on maxillae (Fig. 3). Also, the spermathecae have cactoid lobes at 2/3 distal end of the stalk, outer lobe with constriction at the base and with a notch on inner side toward the distal end (Fig. 6); perfect 'Y' shape, deep burrow with firm silk lining inside the burrow, and distance between the two entrances of the trapdoor nest is twice their diameter (Fig. 7). Male unknown.



Figures 1-7.—*Diplothele graveleyi* new species, female from Angul. 1. Cephalothorax and abdomen, dorsal view; 2. Eyes; 3. Sternum, labium, maxillae and chelicerae; 4. Right chelicera, prolateral face; 5. Abdomen, ventral view; 6. Spermathecae; 7. Burrow. Scale bars: (1-6) 1 mm; (7) 10 mm.

Etymology.—The species is named after the famous arachnologist, Dr. Frederic Henry Gravely (1885–1965). He was Assistant Superintendent at the Indian Museum, Calcutta for a few years and later worked as the Superintendent of the Madras Museum from 1920–1940. He published several monographs and papers on various subjects. He was the first arachnologist to study spiders in the wild in southern and eastern India and described many new species. The specimens collected by him are deposited at the Indian Museum, Calcutta, and Madras Museum. This is a tribute to his contribution to studies on Indian mygalomorph spiders.

Description of female holotype.—Total length 16.90. Carapace 7.46 long, 6.00 wide. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 4.48, 3.86, 4.24, 2.48, 2.10, 17.16. II: 4.40, 3.52, 3.32, 2.46, 2.00, 15.70. III: 4.18, 3.00, 2.72, 3.12, 2.10, 15.12. IV: 6.20, 3.92, 4.72, 5.00, 2.52, 22.36. Palp: 4.10, 2.96, 2.28, –, 2.86, 12.2. Midwidths: femora I = 1.44, II = 1.70, III = 1.72, IV = 1.30, palp = 1.34; tibia I–II = 1.30, III = 1.48, IV = 1.26, palp = 1.28. Abdomen 9.44 long, 6.20 wide. Spinnerets: PLS, total length 2.90 (1.70 basal, 0.80 middle, 0.40 apical; midwidths 0.80, 0.50, 0.30 respectively), 0.30 apart.

Color in life: Carapace, legs and palp brown. Abdomen yellowish-green with brown chevron marking running from dorsal to lateral sides (Fig. 1). Ventral side, yellowish-green with few small black spots between spinnerets and book lungs (Fig. 5). Color in alcohol paler than fresh specimen.

Carapace covered with blackish-brown and small golden, curved hair; hair more concentrated along interstrial ridges, intermixed with few black bristles on caput. Bristles: 10 long on caput in mid-dorsal line; three long, five short anteromedially; six long, several short between PME; one long, two short between AME; one long, five short on clypeus edge. Fovea deep, slightly procurved. Two glabrous bands emerging from fovea and passing on either side of caput.

Eyes: Group occupies 0.30 of head-width; ocular group front width; midwidth; back width; length: 1.00, 1.15, 1.30, 1.30, respectively. Anterior row strongly procurved, posterior row straight; posterior eyes opaque, rest transparent. MOQ front width 0.70, back width 0.80, length 0.60. Diameter of AME 0.30, ALE 0.50, PME 0.10, PLE 0.40. Eye interspaces: AME–AME 0.05, AME–ALE 0.10, ALE–ALE 0.15, PME–PLE adjacent, PME–PME 0.60, ALE–PLE 0.40.

Chelicerae: 3.94 long. Prolateral face glabrous, yellowish-orange with few small hairs; eight promarginal teeth and 24 basomesal teeth in 2–3 parallel lines; rastellum on low mound, consists of 27–30 short thick curved spines, of which 20–23 the mound and seven in anterior line, several normal pointed thin spines on dorsal, and vertical face and upward; dorsally two glabrous bands for length.

Labium: 0.90 wide, 0.70 long; labiosternal groove broad with two sigilla joined medially. Cuspsules absent.

Maxillae: 2.20 long in front, 2.70 long in back, 1.30 wide; 3–4 cuspsules on inner angle. Posterior heel slightly produced, anterior lobe distinct.

Sternum: 3.90 long, 3.10 wide. Covered with hair and bristles. Sigilla indistinct.

Legs: brown, moderately hairy; femora III thicker than rest; all legs of similar thickness; preening comb spines on metatarsi III and IV; coxae IV widest; two glabrous bands longitudinal

on femora, patellae and tibiae (very prominent on patellae); leg formula 4123.

Spines: Leg III: pa, p = 2; ti, p = 1, v = 15, r = 1; mt, p = 2, d = 2; leg IV: ti, v = 5+2 broken, r = 2; mt, p = 2, v = 14. Elsewhere absent.

Scopula: Metatarsi I, distal $\frac{3}{4}$, scopuliform hair intermixed with few bristles and hair but no clear division; tarsi I, full, division with 2–3 rows of hairs; metatarsi II, distal half, division with 2–3 rows of setae; tarsi II, full divided with single row of hairs; metatarsi III, $\frac{1}{4}$ distal, divided with 3–4 rows of bristles and spines; tarsi III–IV, full, divided with 5–6 rows of setae; metatarsi IV, few scopuliform hairs $\frac{1}{4}$ distally, intermixed with spines and bristles.

Trichobothria: Tarsi I, seven clavate, 10 short and long filiform in two rows; tarsi II, six clavate, 10 short and long filiform in two rows; tarsi III, seven clavate, 10 long filiform in distal half in two rows; tarsi IV, eight clavate, 8–10 long in distal half in two rows. Clavate trichobothria confined to basal $\frac{1}{4}$ of tarsi.

Claws: Claw tufts on all legs and palp. All claws edentate, claws of legs I and II clearly smaller than on legs III and IV.

Abdomen: Yellowish-cream with brown chevron mark from dorsal to lateral, uniformly covered with short brown hairs intermixed with few black bristles; ventral side, yellowish cream with few brown spots between spinnerets and book lungs, uniformly covered with short brown hair.

Spermathecae: Two, cactoid shape, each stalk with cactoid outer lobe of similar length at $\frac{2}{3}$ distal end, outer lobe curved toward inner side with constriction at base and notch towards distal end (Fig. 6).

Spinnerets: PMS absent. PLS, apical segment dome shape. Covered with golden brown hair.

Morphometry of female paratype.—Total length 14.70. Carapace 5.70 long, 4.32 wide, chelicerae 2.82 long. Sternum, 2.96 long, 2.00 wide. Labium 0.70 long, 1.00 wide. Maxillae 2.40 back length, 1.80 front length, 1.30 wide, two cuspsules in anterior corner. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 3.92, 2.32, 3.16, 1.52, 1.42, 12.34. II: 3.34, 2.40, 2.78, 1.48, 1.38, 11.38. III: 3.28, 2.22, 2.00, 2.16, 1.44, 11.10. IV: 4.22, 2.36, 3.52, 3.96, 2.16, 16.22. Palp: 2.86, 2.00, 1.74, –, 2.20, 8.80. Midwidths: femora I = 0.70, II = 0.84, III = 1.00, IV = 1.06, palp = 0.66; tibia I = 0.92, II = 0.80, III–IV = 0.92, palp = 0.88. Abdomen 9.00 long, 6.34 wide. Spinnerets: PMS, absent; PLS, 1.00 basal, 0.70 middle, 0.40 distal, 2.10 total length, midwidths 0.70, 0.50, 0.30, respectively.

Distribution.—Orissa: Satkosia WLS and nearby areas in Angul district.

NATURAL HISTORY

Diplothele gravelyi was first found along the perennial stream outside the check gate of Satkosia WLS. It was also found all along the trail from Tikarpada to Blaiput, parallel to the River Mahanadi inside the Satkosia WLS. The forest department had burned the vegetation all along this trail, and we noticed many empty trapdoors.

The spider burrows were located in disturbed habitat with teak trees along the trail, about 10–25 m away from the water body. All along the trails the mud embankments were sloped at about 45° with hard soil, rocky in most places (10–30%), and were covered with dry mosses and grasses (40–60%). The

embankments where these spiders were found faced south and west. Though the burrows were patchy in distribution, the patches were common all along the trails. We estimated six burrows per m² area on the mud embankment. Inside the Sanctuary, the burrows of these spiders along the fire line were more abundant, between 8–12 burrows per m².

The burrows (Fig. 7) of these spiders were forked or 'Y' shaped. They consisted of two entrances with individual short chambers leading to a common chamber that was slightly wider at the base like a bulb. Both entrances of the burrow were separated by a space about twice their own diameter and had a wafer-thin circular hinged door. The outer surfaces of the hinged doors were covered with bits of leaf, soil particles, mosses and lichens, camouflaged with the substrate. The mean length of the burrows was 75 mm (range 70–90 mm), of which the main chamber was 30–40 mm long and the rest was the length of the chambers leading to the entrances. The mean diameter of the entrances of burrows (four burrows excavated) of matured individuals was 15 mm (range 10–15 mm). The silk lining in the burrows was not as thick as found in members of the families Ctenizidae and Idiopidae.

Diplothele tenebrosus new species

Figs. 8–14

Type specimens.—INDIA: Orissa: holotype female, Jadeshwar, Huma, Ganjam district, 144 m elev., 19°44'N, 85°06'E, 19 August 2007, S. Behera, G. Sahu, S. Kumar and M. Siliwal (WILD-07-ARA-244); 2 paratype females, same data as holotype (WILD-07-ARA-201, 245).

Other material examined.—INDIA: Orissa: 1 juvenile, near Berbera-Dhuanali reserve forest, Balugaon, Puri district, 17 April 2007, M. Siliwal, S. Kumar and S. Behera (WILD-07-ARA-189).

Diagnosis (female).—Differs from *Diplothele halyi* and resembles *D. walshi* and *D. gravelyi* by having metatarsi longer than tarsi of all legs. It differs from *D. halyi* and *D. walshi* by having large body size (about 1.6–2.9 times larger). It differs from *D. walshi* and *D. gravelyi* in spermathecal stalks being broader at the base and gradually narrowing towards apex with outer lobe at 2/3 distal end of the stalk, outer lobe of balloon shape with constriction at the base (Fig. 13); single entrance trapdoor burrow (Fig. 14). Male not known.

Etymology.—The word *tenebrosus* in Latin means 'dark', which refers to the darker color of the spider in life.

Description of female holotype.—Total length 20.66. Carapace 10.40 long, 7.72 wide. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 6.1, 4.7, 4.92, 3.8, 2.62, 22.14. II: 6.0, 4.36, 4.74, 3.52, 2.66, 21.28. III: 5.56, 3.6, 3.32, 4.06, 2.68, 19.22. IV: 7.94, 4.54, 6.08, 6.98, 3.34, 28.88. Palp: 5.2, 3.56, 3.0, —, 3.3, 15.06. Midwidths: femora I = 1.92, II = 2.04, III = 2.28, IV = 1.92, palp = 1.48; tibia I = 1.84, II = 1.62, III = 1.74, IV = 1.86, palp = 1.82. Abdomen 10.26 long, 7.00 wide. Spinnerets: PLS, total length 3.48 (2.00 basal, 1.00 middle, 0.48 apical; midwidths 1.12, 0.78, 0.62 respectively), 0.42 apart.

Color in life: Carapace, legs and palp brown. Abdomen dark brown with faint black chevron marking running from dorsal to lateral sides (Fig. 8). The ventral side is uniformly dark brown without any pattern (Fig. 12). Color in alcohol paler

than fresh specimen and chevron marking clearly visible on dorsal and lateral side of abdomen.

Carapace covered with blackish-brown curved hair; hair more concentrated along the interstrial ridges intermixed with black short and long bristles on caput. Bristles: eight long, nine short on caput in mid-dorsal line; two long, two short anteromedially; 10 long, nine short between PME; nine long, eight short between AME; six long, one short on clypeus edge. Fovea deep, straight with procurved ends. Several hairs between PME and ALE. Glabrous bands radiating from fovea, very prominent along sides of caput.

Eyes: Group occupies 0.27 of head-width; ocular group front width, midwidth, back width, length, 1.20, 1.30, 1.50, 1.50 respectively. Anterior row strongly procurved, posterior row straight, posterior medians opaque, rest transparent. MOQ front width 1.00, back width 1.20, length 0.80. Diameter of AME 0.40, ALE 0.60, PME 0.10, PLE 0.70. Eye interspaces: AME–AME 0.20, AME–ALE 0.15, ALE–ALE 0.50, PME–PLE adjacent, PME–PME 0.80, ALE–PLE 0.50.

Chelicerae: 5.86 long. Prolateral face glabrous, yellowish-orange with few small hairs; nine promarginal teeth and 20 basomesal teeth in 2–3 parallel lines; rastellum on low mound, consists of 39–42 short thick curved spines, of which 30–32 on the mound and 9–10 in anterior line, several normal pointed thin spines present on dorsal and vertical face and upward; two glabrous bands longitudinal on dorsal surface of chelicerae.

Labium: 1.46 wide, 1.32 long. Labiosternal groove shallow, broad with two indistinct sigilla on either side. Cuspules absent.

Maxillae: 3.04 long in front, 3.72 long in back, 2.42 wide; three (two large and one small) cuspules on inner angle. Posterior heel slightly produced, anterior lobe distinct.

Sternum: 5.40 long, 4.12 wide, covered with bristles. Sigilla indistinct, all marginal.

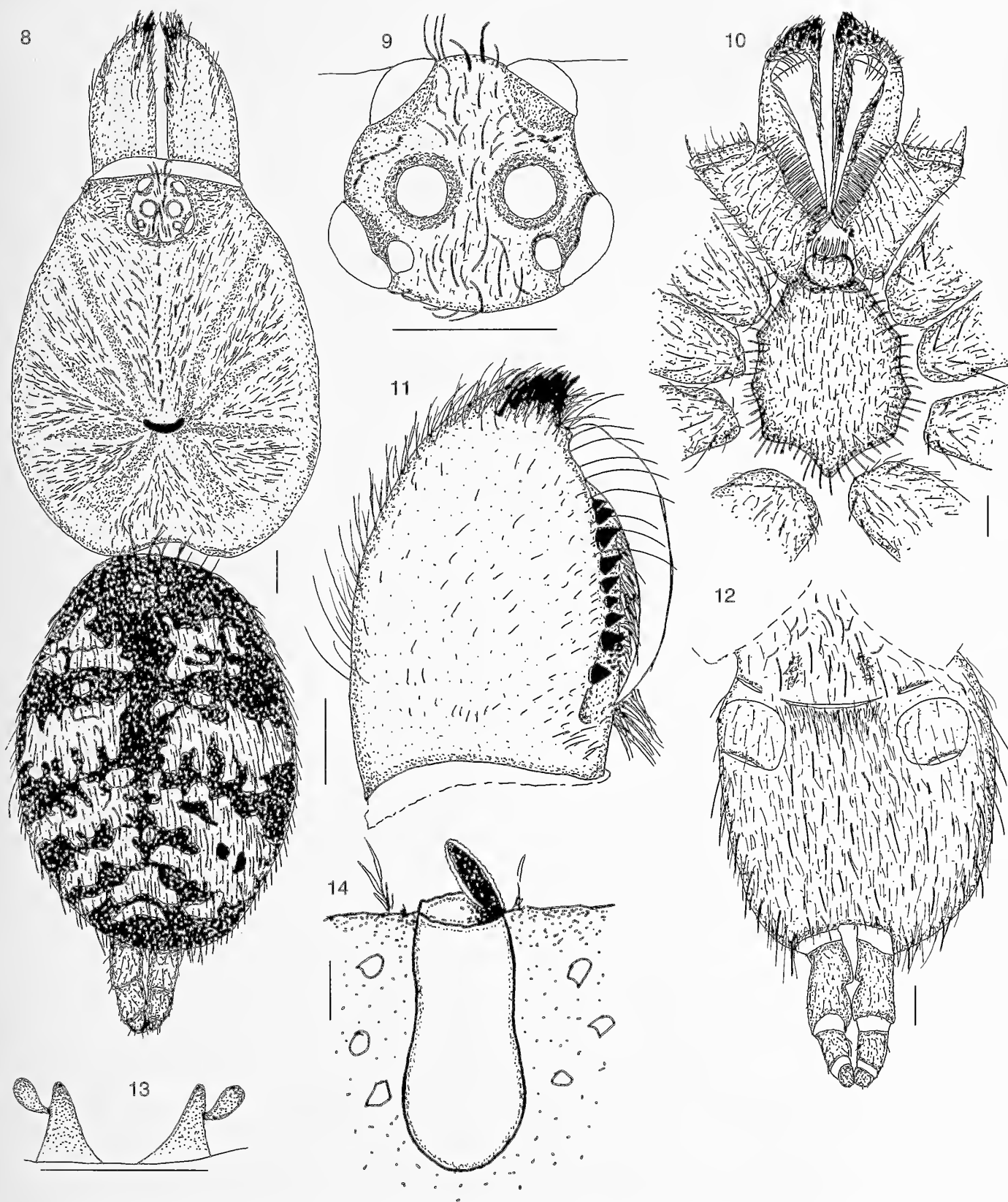
Legs: Uniformly brown, moderately covered with bristles and hairs; femora III thicker than rest; all legs of similar thickness; preening comb spines on metatarsi III and IV; coxae IV widest; two glabrous bands longitudinal on femora, patellae and tibiae (very prominent on patellae); leg formula 4123.

Spines: Leg III: ti, v = 4 + 6 distal, mt, p = 2, v = 8 + 9 distal, r = 2; leg IV: ti, p = 1, v = 4 + 6 distal, r = 2; mt, p = 2, v = 8 + 9 distal, r = 2. Elsewhere absent.

Scopula: Metatarsi I, distal ¾ with few bristles dividing at base; tarsi I, full, division with 2–3 rows of hairs in distal half; metatarsi II, ¾, division with single row of setae; tarsi II, full divided with single row of setae in distal half, basal half with hairless band; metatarsi III, ½ distal, divided with three rows of spines; tarsi III, full, divided with 5–6 rows of small setae; metatarsi IV, ¼ few scopuliform hairs distally, divided by 2–3 rows of setae; tarsi IV, full, divided with 8–9 rows of setae.

Trichobothria: Tarsi I, nine clavate, 12 long and short filiform in two rows in distal half; tarsi II, 11 clavate, 14 long and short filiform in two rows distal half; tarsi III, nine clavate, 10 long filiform in distal half in two rows; tarsi IV, nine clavate, 10 long filiform in distal half in two rows. Clavate trichobothria confined to basal ¼ of tarsi.

Claws: Claw tufts present on all legs and palp. All claws edentate, claws of legs I and II clearly smaller than on legs III and IV.



Figures 8–14.—*Diplothele tenebrosus* new species, female from Jadeshwar. 8. Cephalothorax and abdomen, dorsal view; 9. Eyes; 10. Sternum, labium, maxillae and chelicerae; 11. Left chelicera, prolateral face; 12. Abdomen, ventral view; 13. Spermathecae; 14. Burrow. Scale bars: (8–13) 1 mm; (14) 10 mm.

Abdomen: Dorsally dull cream with irregular dark-brown chevrons running from dorsal to lateral, uniformly covered with short brown hairs intermixed with few black bristles; ventral side, uniformly dull cream, covered with short brown hair.

Spermathecae: Two, stalk broader at base, gradually narrowing towards apex, each stalk with a pair of cactoid outer lobes of similar length at 2/3 distal end, outer lobe balloon shaped with constriction at base (Fig. 13).

Spinnerets: PMS absent. PLS, apical segment dome-shape. Covered with golden brown hair.

Morphometry of female paratypes, WILD-07-ARA-201 (WILD-07-ARA-245).—Total length 21.62 (17.00). Carapace 10.00 (8.68) long, 7.68 (6.44) wide, chelicerae 4.38 (3.70) long. Sternum, 5.00 (3.86) long, 3.76 (3.58) wide. Labium 1.12 (1.00) long, 1.48 (1.28) wide. Maxillae 3.74 (2.54) back length, 2.68 (2.00) front length, 2.22 (1.56) wide, 1–2 cuspules in anterior corner. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 6.0 (4.86), 4.32 (3.94), 4.7 (3.72), 3.08 (2.56), 2.48 (2.06), 20.58 (17.14). II: 6.0 (4.82), 4.22 (3.68), 4.1 (3.42), 3.08 (2.72), 2.48 (2.0), 19.88 (16.64). III: 5.06 (4.32), 3.34 (3.2), 3.04 (2.36), 3.96 (2.98), 2.58 (2.0), 17.98 (14.86). IV: 7.54 (5.94), 4.26 (4.0), 5.62 (4.66), 6.76 (5.38), 2.76 (2.42), 26.94 (22.4). Palp: 4.14 (3.64), 3.12 (2.72), 2.0 (2.16), – (–), 3.62 (2.32), 12.88 (10.84). Midwidths: femora I = 1.76 (1.32), II = 1.78 (1.5), III = 2.12 (1.78), IV = 1.62 (1.32), palp = 1.32 (1.0); tibia I = 1.74 (1.34), II = 1.74 (1.0), III = 1.42 (1.0), IV = 1.62 (1.38), palp = 1.64 (1.26). Abdomen 11.62 (8.00) long, 8.32 (5.46) wide. Spinnerets: PMS, absent; PLS, 2.00 (1.92) basal, 1.20 (0.90) middle, 0.72 (0.68) distal, 3.92 (3.50) total length, midwidths 1.12 (0.86), 0.78 (0.66), 0.70 (0.50) respectively.

Distribution.—Orissa: Jadeshwar, Huma in Ganjam district; Near Berbera-Dhuanali reserve forest, Balugaon, Puri district.

NATURAL HISTORY

These spiders were found in an undisturbed mango orchard with weeds covering 90% of ground. The burrows were constructed on the ground or roadside mud embankments; the soil was easy to dig because of recent rain. Due to dense undergrowth, we could not estimate the density of this spider in this area, but we estimated seven burrows per m² area on the roadside embankments.

The burrow structure (Fig. 14) was a simple trapdoor, a single entrance leading to a short chamber that was wider at the base. The burrow was lined with a thick layer of off-white silk as seen in the burrow of *D. gravelyi* new species; however, the silk was firm and did not break. We had to use a pair of scissors to take a cross-section of the burrow silk. The entrance had a circular wafer-thin hinged door, whose outer surface was covered with soil particles, camouflaging it in the surrounding. The mean length of the burrow (six burrows excavated) was 60 mm (range 60–80 mm). The diameter of the entrances of the burrows ranged between 15–20 mm (mean 15 mm). In Jadeshwar, these spiders were found making vertical burrows on ground, whereas in Balugaon, they were found in horizontal burrows on roadside embankments. At the slightest disturbance, these spiders jumped out of the burrow and disappeared in the nearby vegetation or leaf litter.

Diplothele walshi O. Pickard-Cambridge 1890

Figs. 15–21

Diplothele walshi O. Pickard-Cambridge 1890:621.

Adelonychia nigrostriata Walsh 1891:269. First synonymised by Gravely (1915).

Neotype.—INDIA: Orissa: neotype female, Barkuda Island, Chilika lake, Orissa, 133 m, 19°55'N, 85°15'E, 18 August 2007, S. Behera, M. Siliwal and G. Sahu (WILD-07-ARA-195).

Other material examined.—INDIA: Orissa: 1 female, same data as neotype (WILD-07-ARA-196); 2 juveniles, same data as neotype (WILD-07-ARA-197, 241).

Diagnosis (female).—Differs from *Diplothele halyi* by having metatarsi longer than tarsi of all legs, distinct abdominal pattern and fovea larger (Pocock 1900). It differs from the two new species in absence of maxillary cuspules (Fig. 17); smaller in size; shallow, forked double entrance trapdoor burrow made up of very flimsy silk, which breaks while excavating the burrow (Fig. 21). Male not known.

Description of female neotype.—Total length 10.60. Carapace 4.86 long, 3.34 wide. Chelicerae 1.82 long. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 2.3, 1.76, 1.58, 1.0, 0.92, 7.56. II: 2.04, 1.5, 1.42, 1.0, 0.88, 6.84. III: 2.0, 1.38, 0.98, 1.0, 0.9, 6.26. IV: 2.58, 1.8, 2.0, 2.12, 1.32, 9.82. Palp: 1.46, 1.18, 0.9, –, 1.3, 4.8. Midwidths: femora I–II = 0.70, III = 1.0, IV = 0.8, palp = 0.6; tibia I–II = 0.62, III = 0.72, IV = 0.76, palp = 0.6. Abdomen 5.74 long, 4.00 wide. PLS, total length 1.66, (0.80 basal, 0.60 middle, 0.26 apical; midwidths 0.60, 0.40, 0.30 respectively), 0.20 apart.

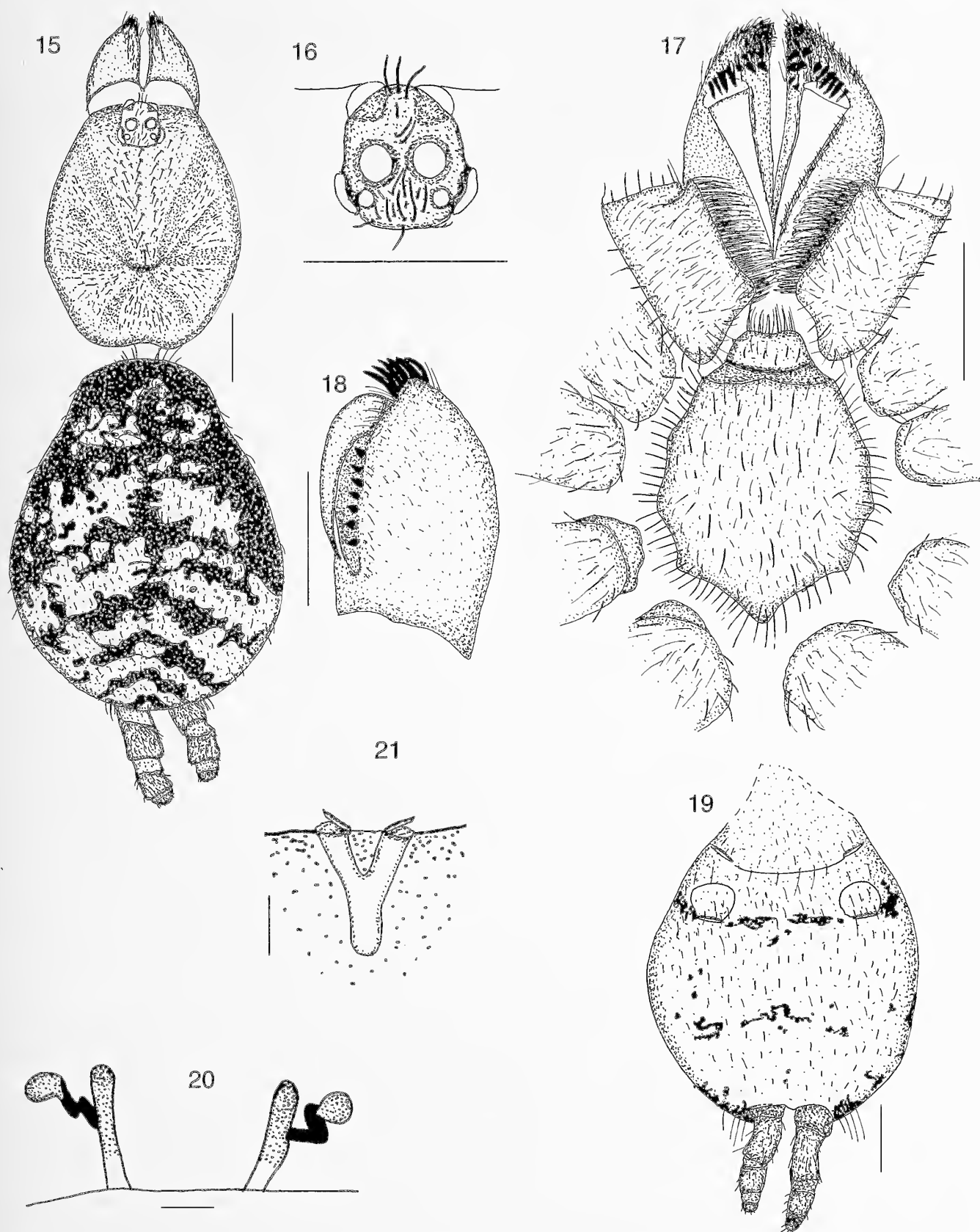
Color in alcohol: Carapace, legs and palp yellowish-brown. Abdomen yellowish-cream, dorsally with irregular brown chevron marking running from dorsal to lateral sides (Fig. 15). Ventral side, yellowish-cream with few small brown spots and blotches between spinnerets and book lungs (Fig. 19).

Carapace covered with blackish-brown hair; few short and long black bristles on caput. Bristles: nine long, two short on caput in mid-dorsal line; two long, one short anteromedially; eight long, 12 short hairs between PME; four long, two short between ALE and clypeus edge. Fovea deep, straight with procurved ends. Interstitial ridges prominent, radiating from fovea.

Eyes: Group occupies 0.30 of head-width; ocular group front width, mid width, back width, length, 0.70, 0.90, 1.10, 0.80 respectively. Eyes in three rows, posterior row almost straight; posterior eyes opaque, rest transparent. MOQ front width 0.70, back width 0.80, length 0.50. Diameter, AME 0.30, ALE 0.40, PME 0.10, PLE 0.50. Eye interspaces: AME–AME 0.05, AME–ALE 0.10, ALE–ALE 0.20, PME–PLE adjacent, PME–PME 0.60.

Chelicerae: 2.36 long intact. Prolateral face glabrous, yellowish-orange with few small hairs; seven promarginal teeth and 12 basomesal teeth in 2–3 parallel lines. Rastellum on low mound, consists of nine short, thick, curved spines of which seven on mound and two in anterior line, accompanied by several pointed thin spines on dorsal, vertical face and upwards; two glabrous bands longitudinal on dorsolateral surface of chelicerae.

Labium: 0.60 wide, 0.40 long. Labiosternal groove shallow, broad with inconspicuous sigilla on either side, raised in center. Cuspules absent.



Figures 15–21.—*Diplothele walshi*, female from Barkuda Island. 15. Cephalothorax and abdomen, dorsal view; 16. Eyes; 17. Sternum, labium, maxillae and chelicerae; 18. Right chelicera, prolateral face; 19. Abdomen, ventral view; 20. Spermathecae; 21. Burrow. Scale bars: (8–13) 1 mm; (14) 10 mm. Scale bars: (15–19) 1 mm; (20) 0.1 mm; (21) 10 mm.

Maxillae: 1.10 long in front, 1.50 long in back, 0.80 wide; cuspules absent. Posterior heel slightly produced, anterior lobe short.

Sternum: 1.90 long, 1.60 wide. Sigilla indistinct.

Legs: uniformly yellowish-brown, covered with bristles and hairs; femora III thicker than rest; all legs of similar thickness; preening comb present on metatarsi III and IV; coxae IV widest; two glabrous bands running longitudinal on femora, patellae and tibiae (very prominent on patellae); leg formula 4123.

Spines: Leg III: pa, p = 5; ti, p = 1; mt, p = 3, r = 1, v = 6+10 distal; leg IV: mt, p = 2, r = 2, v = 10 distal. Elsewhere absent.

Scopula: Metatarsi I, $\frac{1}{2}$ distal, scopulae not dense intermixed with few bristles; tarsi I, full, division with 2–3 rows of thin bristles; metatarsi II, distal half, rudimentary, scopuliform hair intermixed with few bristles; tarsi II, full, divided with 3–4 rows of bristles; metatarsi III, $\frac{1}{4}$ distal, few scopuliform hairs intermixed with bristles and spines; tarsi III, full, divided with 6–7 rows of setae; metatarsi IV, few scopuliform hair distally; tarsi IV, full, divided with 6–7 rows of setae.

Trichobothria: Tarsi I, six clavate, 10–12 long and short filiform in two rows, for length; tarsi II, five clavate, 10 long and short filiform in two rows in v-shape; tarsi III, one (rest broken) clavate, 10 long filiform in distal half in two rows; tarsi IV, four clavate, 10 long in distal half in two rows. Clavate trichobothria confined to about basal $\frac{1}{4}$ length of tarsi. Filiform in distal half on all tarsi in v-shape.

Claws: Claw tufts present on all legs and palp. All claws edentate, claws of legs I and II clearly smaller than on legs III and IV.

Abdomen: Cream with prominent irregular chevron marking running from dorsal to lateral sides; uniformly covered with short brown hairs. Ventrally cream with brown spots and blotches between spinnerets and book lungs.

Spermathecae: Two, finger-like, each stalk with outer lobe at distal half, outer lobe with sclerotized and twisted stalk (Fig. 20).

Spinnerets: PMS absent. PLS, covered with golden brown hair, apical segment dome-shaped.

Morphometry of female (WILD-07-ARA-196) (Table 1).—Total length 7.42. Carapace 2.94 long, 2.46 wide. Chelicerae 1.26 long. Sternum, 1.50 long and 1.30 wide. Labium 0.40 long, 0.60 wide. Maxillae 1.20 back length, 0.98 front length, 0.64 wide. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 1.68, 1.40, 1.24, 0.94, 0.88, 6.14. II: 1.46, 1.22, 1.12, 0.92, 0.86, 5.58. III: 1.24, 0.96, 0.88, 0.9, 0.86, 4.84. IV: 1.94, 1.20, 1.56, 1.66, 1.12, 7.48. Palp: broken. Midwidths: femora I = 0.64, II = 0.50, III = 0.78, IV = 0.64, palp = broken; tibia I = 0.56, II = 0.52, III = 0.64, IV = 0.62, palp = broken. Abdomen 4.48 long, 3.40 wide. PLS, total length 1.20 (0.60 basal, 0.40 middle, 0.20 apical; midwidths 0.50, 0.40, 0.20, respectively), 0.18 apart.

Distribution.—Orissa: Barkuda Island, Chilika Lake; Ganjam; Andhra Pradesh: Waltair (=Visakhapatnam) in Madras Presidency.

Remarks.—Roewer (1942:217, 218) incorrectly reported that Pocock (1900:175) had males of both *D. walshi* and *D. halyi*, whereas a male is known only for the latter.

Raven (1985) reported that the holotype of *D. walshi* was lodged in the Hope Collection, Oxford University but in checking with the current curator at the time, Ivor Lansbury, reported it could not be found. Raven, in 1983, also looked for it in a number of other European museums, including the Natural History Museum. We rechecked with the collections manager of the Hope Collection and it was reconfirmed that the type was lost. Our discovery of three species in the state of Orissa made the correct identification of *D. walshi* essential. The original locality given by O. Pickard-Cambridge (1890) was “Orissa, Calcutta” and the holotype was an immature female; the neotype is from that state. However, Calcutta is not in Orissa state, but as with many of these early collections, it is assumed that the published locality is a combination of the port of exit or the home of the collector. In this case, the collector was at the Calcutta Hospital (in West Bengal) and thus it is assumed that the spider’s locality was the adjacent state of Orissa.

NATURAL HISTORY

These spiders were collected from Barkuda Island, Chilika Lake, southern Orissa. The vegetation on the Barkuda Island mainly consists of thorny shrubs (mainly *Acacia* spp. and *Ziziphus* spp.), cactus, and a few young trees. The burrows were constructed at the base of shrubs on the ground, amongst the roots in the loose soil. Burrows were very easy to dig as the soil was sandy. This spider seems to be very common on the island; in 30 minutes we found four spiders. Due to dense vegetation, we could not estimate the density of this spider population on the island.

The burrow structure (Fig. 21) was fork-shaped with two entrances leading to a short common chamber. The burrow was lined with silk, not as thick as that of *D. gravelyi* and *D. tenebrosus*, and being weak, broke on digging. Both entrances had circular, wafer-thin, hinged doors, their distance apart being about the diameter of an entrance. The outer surface of these hinged doors was covered with soil particles and bits of dry leaves, camouflaging it in the surrounding. The mean length of the burrow was 25 mm (range 15–25), of which the main chamber was about 8–10 mm long and the remainder was the length of the chambers leading to entrances. Diameter of the burrow entrances ranged between 6–7 mm (mean = 7 mm), similar to that reported by Gravely (1921).

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LITERATURE CITED

- Gravely, F.H. 1915. Notes on Indian mygalomorph spiders. Records of the Indian Museum, Calcutta 11:257–287.
- Gravely, F.H. 1921. The spiders and scorpions of Barkuda Island. Records of the Indian Museum, Calcutta 22:399–421.
- Gravely, F.H. 1935. Notes on Indian mygalomorph spiders. II. Records of the Indian Museum, Calcutta 37:69–84.
- Pickard-Cambridge, O. 1890. On some new species and two new genera of Araneida. Proceedings of the Zoological Society of London 1890:620–629.
- Platnick, N.I. 2008. The World Spider Catalog, Version 8.5. American Museum of Natural History, New York. Online at <http://research.amnh.org/entomology/spiders/catalog/index.html>
- Pocock, R.I. 1900. The Fauna of British India, Including Ceylon and Burma. Arachnida. Taylor and Francis, London. Pp. 1–279.
- Raven, R.J. 1985. The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. Bulletin of the American Museum of Natural History 182:1–180.
- Roewer, C.F. 1942. Katalog der Araneae von 1758 bis 1940. Paul Budy, Bremen. Pp. 1–1040.
- Siliwal, M. & S. Molur. 2007. Checklist of spiders (Arachnida: Araneae) of South Asia including 2006 update of Indian spider checklist. Zoos' Print Journal 22(2):2551–2597 (plus 84 p. web supplement).
- Simon, E. 1892. Histoire naturelle des araignées. Librairie Encyclopédique de Roret, Paris 1:1–256.
- Walsh, J.H.T. 1891. A new trap-door spider from Orissa. Journal of the Asiatic Society of Bengal 59:269–270.

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A review of the pirate spiders of Tasmania (Arachnida, Mimetidae, *Australomimetus*) with description of a new species

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Abstract. A new pirate spider (family Mimetidae) is described as *Australomimetus mendax* new species from Tasmania, Australia. In this context, all mimetid species currently known from the island have been reviewed and re-illustrated. Five species are recorded and they all belong to the genus *Australomimetus* Heimer 1986. Re-illustrated here are *Australomimetus maculosus* (Rainbow 1904), *A. tasmaniensis* (Hickman 1929) new combination, *A. aurioculatus* (Hickman 1929) new combination and *A. audax* (Hickman 1929) new combination. We briefly discuss the phylogenetic relationships of these species and provide distribution maps of their Tasmanian records. *Australomimetus mendax* is the only species currently endemic to Tasmania. All other species exhibit wide distribution patterns from tropical Queensland to Western Australia. The ranges of *A. aurioculatus* and *A. audax* – species originally thought to be Tasmanian endemics – are now extended to include the Australian mainland as well. The cosmopolitan genus *Mimetus* Hentz 1832 is restricted and excludes all pirate spiders with a Tasmanian distribution.

Keywords: Araneomorphae, *Australomimetus*, Entelegynae, *Ero*, *Mimetus*

Spiders of the family Mimetidae have long been recognized for their conspicuous araneophagic feeding ecology (Wiehle 1953; Cutler 1972; Jackson & Whitehouse 1986; Kloock 2001). They are also notable for the controversies and conflicting hypotheses concerning their systematic affinities, with some authors suggesting placement in the superfamily Palpimanoidea (Forster & Platnick 1984; Coddington et al. 2004) or, alternatively, the superfamily Araneoidea (Schütt 2000, 2003; Griswold et al. 2005). There has been no broad taxonomic treatment of the family since Platnick and Shadab's (1993) revision of the species of Chile which represented a first modern attempt to delimit the South American genera. Some additional revisions or taxonomic treatments have since been published, but remain regional in focus (Thaler et al. 2004; Barrion & Litsinger 1995; Paquin & Dupérré 2003). The Australian fauna has not yet been studied using modern methods of phylogenetic reconstruction and, as with many other spiders, the Australian mimetids have had a checkered taxonomic history due in part to the rareness of specimens in museum collections and the lack of published studies on ecology and distribution.

The first Australian mimetid – *Australomimetus maculosus* (Rainbow 1904) – was described from New South Wales and placed, with reservations, within the cosmopolitan genus *Mimetus* Hentz 1832 by Rainbow (1904), who drew on the generic concept outlined by Simon (1892–1895). Similar species had already been described from New Zealand and placed incorrectly at the family level in taxa such as *Linyphia* Latreille 1804 (Linyphiidae) (Urquhart 1891) or alternatively in *Mimetus* (Cambridge 1879; Bryant 1935).

Before the rich spider fauna of the Australian mainland began to attract detailed attention, three mimetids were described from Tasmania and were also assigned either to *Mimetus* or *Ero* C.L. Koch 1836 – the latter representing the second cosmopolitan genus within the family (Hickman 1929).

These generic designations remained doubtful since the Australian species did not fit comfortably into Simon's classical concept of mimetid genera, however, Hickman and other early authors preferred not to raise new genera. Furthermore, it was obvious that more undescribed species were still to be found in Tasmania (Hickman 1967). Although the mimetid fauna of both the Australian mainland, and the island of Tasmania, appeared to be unusually diverse for such a small spider family – which currently includes some 160 species (Platnick 2008) – no broad taxonomic treatment of the Australian species was published until the description of 17 additional species from Queensland and New South Wales by Heimer (1986). In this study the new genus *Australomimetus* Heimer 1986 was raised to accommodate these new species and '*Mimetus*' *maculosus* from the Australian eastcoast became the type species (Heimer 1986). The new genus was based solely on a single, 'absence' character: the lack of a shovel-like appendage on the dorsal edge of the cymbium whose presence was reported as characteristic for *Mimetus* (compare Heimer 1986, fig. 1 with fig. 11). The restrictive nature of this concept became obvious when Heimer (1989) described some new species as *Mimetus*, even though these species are very similar to the type species of *Australomimetus* in somatic appearance and genital morphology. Practical problems also arose from the poor quality of his descriptions and drawings, to the extent that identifying individual specimens became almost impossible. Even Heimer himself confused individual species (Harms & Harvey, in press). Finally, the New Zealand pirate spiders remained in *Mimetus*, although the need for revision of the New Zealand fauna was noted, with some authors suggesting that their current placement is only preliminary (Forster & Forster 1999).

Recently, the mimetid fauna of Western Australia was investigated for the first time, both phylogenetically and taxonomically (Harms & Harvey, in press). A cladogram for

the Australian species based on comparative morphology will be presented elsewhere (Harms & Harvey, in press). A preliminary higher level phylogeny for the whole family and its generic structure is also being prepared (Harms & Harvey, in prep.). It now appears that all mimetids from Australia, New Zealand and New Caledonia do form a monophyletic group which is distinct from *Mimetes* and for which the generic name *Australomimetes* can be applied. It will also be shown that neither *Mimetes* nor *Ero* are native to Australia or New Zealand and that all species from Australia and New Zealand currently attributed to one of these supposedly cosmopolitan genera are in fact misplaced. This also holds true for all species from Tasmania which are all assigned in the present paper to *Australomimetes*.

Whilst examining extensive collections of Mimetidae from mainland Australia, some new records of mimetid species previously only known from Tasmania were found. Detailed study revealed five Tasmanian species in total – an increase of two species since Hickman (1929). Additionally, a new species from Tasmania is described here. This present revision permits accurate identification of all known Tasmanian mimetids. We provide the first detailed drawings for all species and redescribe individual species in cases where the original descriptions are poor. An identification key is provided, incorporating the generic transfers proposed here. Distribution maps are also provided and species-relationships are briefly discussed. The phylogenetic analysis of *Australomimetes* will be published elsewhere, as will redescrptions of some of the species from the Australian mainland (Harms & Harvey, in press). This present study is intended as a contribution towards elucidating the rich alpha-diversity of Australian pirate spiders.

METHODS

All specimens were examined and illustrated in 70% ethyl alcohol. Female genitalia were dissected with a sharp needle and cleared from surrounding tissue by immersing the dissected structure in a warmed solution of 10% potassium hydroxide, when necessary. Male palpal organs were expanded by immersion in 10% potassium hydroxide at room temperature for several minutes and transferring them back and forth between KOH and distilled water until the desired expansion took place. Measurements were taken using a graticule calibrated in millimetres. Illustrations were produced using a combination of a camera lucida and photographs taken with a Canon G6[®]. Digital image manipulation was carried out using Adobe Photoshop 7.0[®]. Text figures were prepared using CorelDRAW[®] Version 9.0. Maps were generated using ArcView[®] Version 3.1 after conversion of Excel-files into D-Base IV formats.

The specimens listed in this study are lodged in the following institutions: Australian Museum, Sydney, Australia (AM); Muséum d'Histoire Naturelle, Genève, Switzerland (MHNG); Queensland Museum, Brisbane, Australia (QM); Queen Victoria Museum, Launceston, Australia (QVM); Western Australian Museum, Perth, Australia (WAM).

The following abbreviations are used throughout the manuscript. Eyes: AME = anterior median eyes; ALE = anterior lateral eyes; LE = lateral eyes; ME = median eyes; MOQ = median ocular quadrangle; PME = posterior median

eyes; PLE = posterior lateral eyes. Epigynum: BP = basal plate, ID = insemination duct, R = receptaculum. Male pedipalp: CY = cymbium, DMS = distomedial sclerite of the embolic division, E = embolus, MES = medioectal sclerite of the embolic division, PA = pedipalpal patella, PBL = paracymbial basal lobe, PC = paracymbium, PML = paracymbial medial lobe, ST = subtegulum, TE = tegulum, TI = pedipalpal tibia, TR = trichobothria of the male pedipalpal tibia, TSD = tegular sperm duct. Spinnerets: AS = anterior spinnerets; PLS = posterior lateral spinnerets; PMS = posterior median spinnerets. Spigots: AC = aciniform gland spigot(s), CO = colulus, CY = cylindriform gland spigot(s), PI = pyriform gland spigot(s), SH = serrate hairs.

SYSTEMATICS

Family Mimetidae Simon 1881

Genus *Australomimetes* Heimer 1986

Australomimetes Heimer 1986:115; Platnick 1989:169.

Mimetes Hentz 1832: Rainbow 1904:330 (in part); Hickman 1929:107 (in part); Roewer 1942:1021 (in part); Bonnet 1957:2917, 2920 (in part); Hickman 1967:50 (in part); Platnick 1993:155 (in part).

Ero C.L. Koch: Hickman 1929:114 (in part); Roewer 1942:1019 (in part); Bonnet 1956:1799 (in part); Heimer 1986:135 (in part); Platnick 1989:171 (in part); Platnick 1993:154 (in part).

Type species.—*Mimetes maculosus* Rainbow 1904, by original designation.

Diagnosis.—Species of *Australomimetes* possess a unique conformation of the male pedipalp. There is a massive, but simple sclerite in a distal position (DMS) which serves as a functional conductor and is often adorned with additional sclerotizations in medioectal position (MES) (Figs. 5a–c; 8a–b, 11c). The cymbium is always slender and lacks additional sclerotizations or distinct retrolateral sclerotizations (e.g. Figs. 8a–b). The paracymbium is usually elongate, well-pronounced and can contain additional lobes or sclerotizations (Figs. 2d, 11b). Females of the genus have cylindriform gland spigots on the posterior spinnerets which are enlarged and rotund. They are smooth and lack any incisions (Fig. 3a–b). Males of *Australomimetes* can be distinguished from the closely related genera *Mimetes* and *Phobetinus* in lacking a retrolateral extension of the cymbial margin (“shovel”) and in possessing a well-pronounced, elongate paracymbium (compare e.g. Paquin & Dupérré 2003, figs. 1946, 1149, 1952 with Figs. 5e–f or 8a–b). Females of *Australomimetes* can be distinguished from females of *Ero* and *Mimetes* in lacking the conspicuous incisions on the enlarged and rotund cylindrical gland spigots (Figs. 3a–b). The cylindriform gland spigots in *Australomimetes* also appear to be more slender.

Description.—Small to medium sized, araneomorph spiders (5–15 mm).

Eyes: eight heterogeneous eyes; AME largest and moderately protuberant; ALE and PLE protuberant and juxtaposed, secondary eyes with tapetum; two spines between AME (Figs. 2c, 5d, 11a; also Forster & Platnick 1984, fig. 378).

Clypeus: narrow and about AME diameter; with small solitary setae in a typical arrangement (one seta halfway between AME and suture of palpuron; 4 setae median at suture

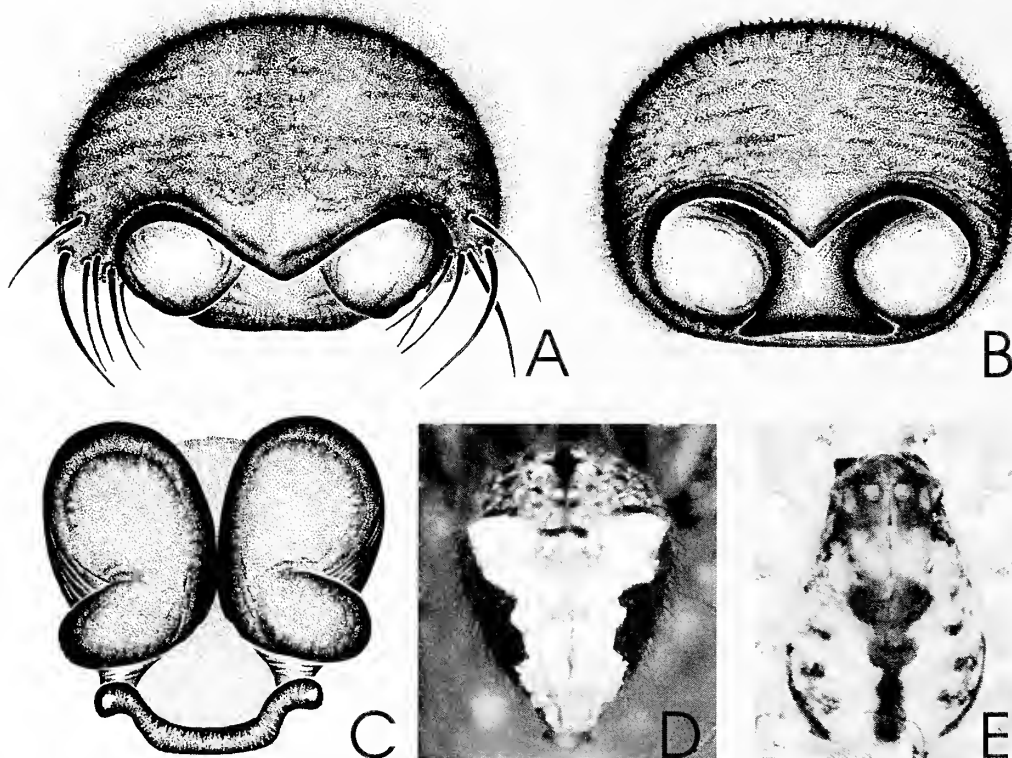


Figure 1.—*Australomimetes audax*, female holotype. A. Epigynum, ventral view; B. Same, posterior view (Note that the epigyne is almost oval in shape.); C. Receptacula; D. Opisthosoma, distal view (Note the presence of a prominent creamy triangular folium with serrated margins.); E. Carapace, frontal view.

of paturon), all setae directed downwards (Forster & Platnick 1984, fig. 377).

Carapace: oval with slightly or strongly attenuated and sloping cephalic region (e.g. Fig. 2c; also Heimer 1986, fig. 17). Cuticle of pars cephalica with three longitudinal rows of spines which extend toward fovea; median line straight, lateral lines directed interior and extending from PE tubercle to fovea (Fig. 5d). Fovea evident, ovoid and slightly depressed; pars thoracica with two fields of small and inconspicuous conical spines.

Chelicerae: paturon elongate and directed vertically, basally fused (Forster & Platnick 1984, fig. 377; also Heimer 1986, fig. 18). Distal promargin adorned with peg teeth; retromargin with one or two small teeth (Forster & Platnick 1984, fig. 381). An evident diastema present (Schütt 2003); cuticle finely reticulated. Labium subtriangular, longer than wide and not rebordered (Forster & Platnick 1984, fig. 382); endites longer than wide with a reddish submarginal serrula.

Sternum: scutiform, longer than wide (e.g. Forster & Platnick 1984, fig. 392).

Legs: formula I, II, IV, III (rarely I, IV, II, III). Forelegs relatively long and armed with spines; tibiae and metatarsi with one to three rows of raptorial spines along the anterior prolateral surfaces, where long erect spines are interspersed by three or four smaller bent ones (e.g. Forster & Platnick 1984, fig. 383). Femora I (retrolateral) and II (prolateral) with a conspicuous longitudinal row of short conical spines; robust species with a similar, but less evident, row on retromargin of femur II (Heimer 1986, fig. 19). Tarsal organ capsulate with round orifice (Griswold et al. 2005). All hairs serrate, cuticle

squamate. Tibiae with two rows of trichobothria (Fig. 8a), metarsi with one trichobothrium in a subapical position and tarsus without trichobothria. Three claws; accessory claws present.

Opisthosoma: broadly oval to slightly triangular. Cuticle with strong, but isolated setae (Fig. 1d); humps may be present, but are not frequent (e.g. Mascord 1970, figs. 65–66). Two booklungs and a single tracheal spiracle anterior to spinnerets.

Pedipalp: female pedipalp with one claw. Male pedipalp with slender and hirsute cymbium without sensory setae; paracymbium elongate, in subbasal position and frequently with secondary sclerotizations or lobes (Figs. 5e–f, 11b–c). Subtegulum and tegulum aligned via haematodocha; tegular sperm duct visible, straight to strongly curved (e.g. Figs. 2a, 5b, 8a, 11c). Distal sclerite (DMS) of pedipalp simple and in median position, broadly fused to tegulum and conducting embolus medially and distally, often with additional sclerotizations in a basal position (e.g. Figs. 2a, 8a–b). Further sclerotizations (MES) may be found medioectally between cymbial tip and DMS (Figs. 8a–b; 9c). Embolus strongly sclerotized, prolonged and twisted around DMS (Figs. 2b, 8b), embolic origin often inserted onto tegulum via a small, triangular sclerotized plate. Palpal tarsus not, or only slightly, twisted; cymbium situated rather distad and not lateral. Pedipalpal patella usually with 3 spines, reductions occur in *A. mendax* new species (2 spines) and *A. tasmaniensis* (Hickman) (1 spine).

Female genitalia: entelegyne but simple, heavily sclerotized with two oval atria and two short, sclerotized insemination

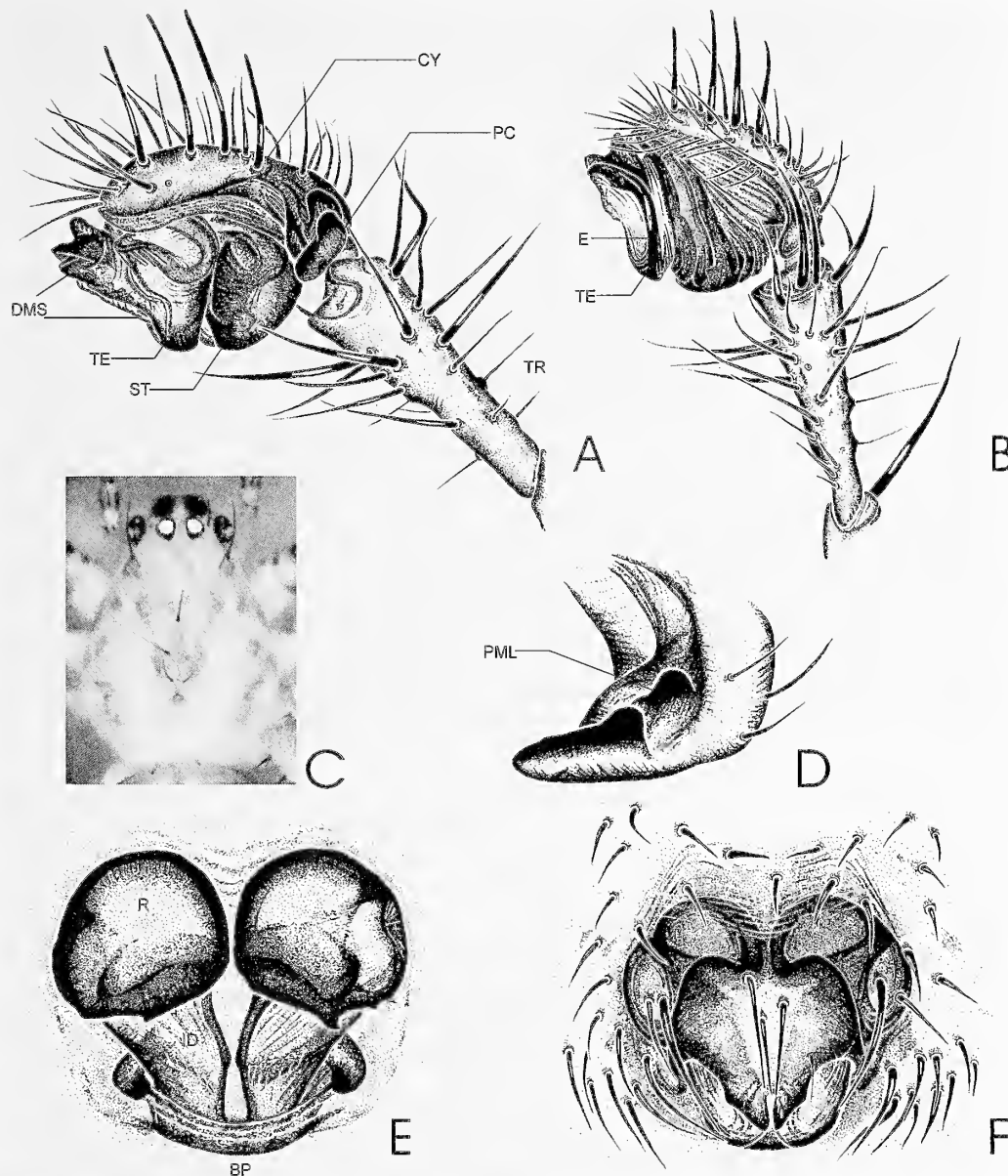


Figure 2.—*Australomimetes auriocolatus*. A. Male pedipalp, retrolateral view; B. same, prolateral view (Note that the tip of the DMS is convex in lateral view and that the tegular sperm duct (TSD) is strongly curved. The cymbium is adorned with a row of strong spines.); C. Female carapace, frontal view; D. Paracymbium, lateral view; E. Receptacula; F. Epigynum, ventral view.

ducts (Figs. 2e, 6b–e). Receptacula strongly sclerotized and thick-walled without additional glandulae; spherical to globular and never with additional lobes (Fig. 6e, also 9e). A small epigynal “scape” might be present (e.g. Heimer 1986, fig. 14).

Spinnerets: ecribellate, six spinnerets present. Colulus present, fleshy and adorned with some setae. AS largest and conical. PLS short and inconspicuous. PMS medium-sized. PLS and PMS with a single cylindriform gland spigot each (Fig. 3b); cylindriform spigots enlarged, rotund and smooth without incisions. Triad absent (Figs 3a–b). Anus adorned with some setae and labellate.

Note that the cylindriform gland spigots differ in shape from those of *Ero* and *Mimetes*. Females of the latter genera possess somewhat bud-shaped cylindriform gland spigots with

longitudinal incisions (Platnick & Shadab 1993, figs. 26–28). Please see Harms & Harvey (in press) for a detailed discussion on spigot structure in *Australomimetes*.

Distribution.—The genus was described first only from Queensland and New South Wales and was thus accordingly endemic to the Australian mainland (Heimer 1986, 1989). However, all species of pirate spiders from Tasmania and New Zealand – currently assigned to either *Mimetes* or *Ero* – will also be referred to this genus (Harms & Harvey, in press). Three additional species from New Caledonia and Indonesia will be described elsewhere as *Australomimetes* and two species from Japan and China also seem to belong here (Harms, in press). Consequently, a predominantly Australasian distribution for the taxon must be assumed, with a distribution range that includes the complete Australian region but also south-

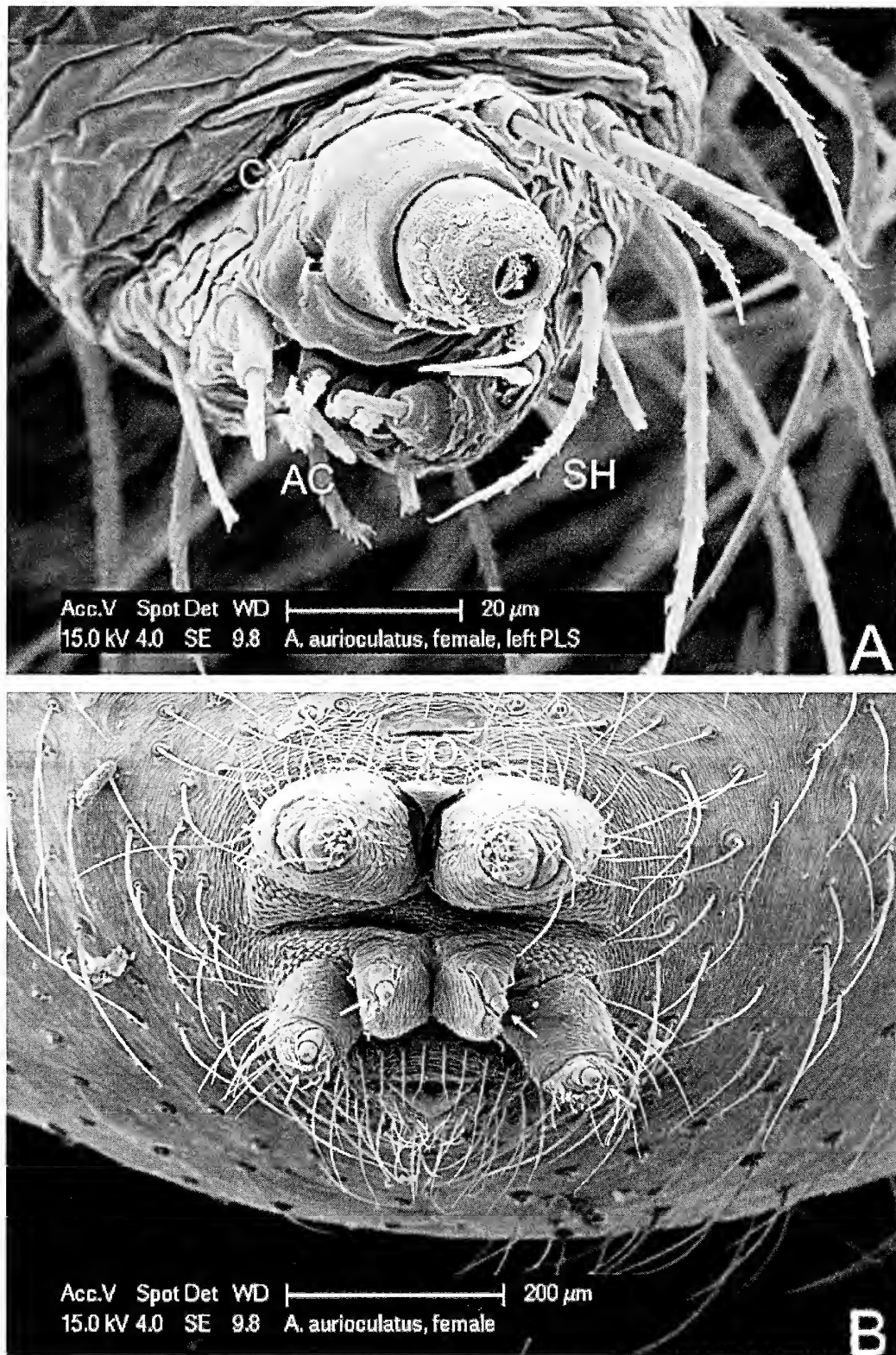


Figure 3.—*Australomimetus aurioculatus*, female. A. Detailed view of posterior lateral spinnerets. The cylindriform gland spigot is rotund and enlarged but lacks any incisions or ridges. B. Overview of spinnerets, ventral view. Arrows point to the position of the cylindriform gland spigots. Note that all posterior spinnerets bear a single, rotund and enlarged cylindriform gland spigot. See also Harms & Harvey (in press) for a detailed discussion of spigot structures in *Australomimetus*.

eastern Asia. In Asia, species of *Australomimetes* exist sympatrically with other genera of Mimetidae: *Phobetinus* Simon, 1895 (south-eastern Asia and India); *Mimetes* (worldwide, except Australia and Antarctica) and *Ero* (also worldwide except Australia and Antarctica). The fauna of Asia is therefore exceptionally rich in genera whereas *Australomimetes* is the only genus native to the Australian region.

Included species.—*Australomimetes andreae* Heimer 1989, *A. annulipes* Heimer 1986, *A. audax* (Hickman 1929) new

combination, *A. aurioculatus* (Hickman 1929) new combination, *A. burnetti* Heimer 1986, *A. childersiensis* Heimer 1986, *A. daviesanus* Heimer 1986, *A. hartleyensis* Heimer 1986, *A. hertelians* Heimer 1986, *A. hirsutus* Heimer 1986, *A. kioloensis* Heimer 1986, *A. maculosus* (Rainbow 1904), *A. mendax* new species, *A. miniatus* Heimer 1986, *A. pseudomaculosus* Heimer 1986, *A. raveni* Heimer 1986, *A. robustus* Heimer 1986, *A. spinosus* Heimer 1986, *A. subspinosus* Heimer 1986, *A. sydneyensis* Heimer 1986, *A. tasmaniensis* (Hickman 1929), *A. triangulosus* Heimer 1986.

KEY TO THE TASMANIAN SPECIES OF MIMETIDAE

The Tasmanian fauna comprises five species of *Australomimetes*, of which one is known from the female only. All have been recently collected from the Australian mainland and only *A. mendax* appears to be truly endemic to Tasmania.

1. Leg formula I IV II III 2
Leg formula I II IV III 3
2. Carapace framed by dark lateral line (Fig. 11a); clypeus higher than AME diameter *A. tasmaniensis*
Opisthosoma with conspicuous whitish dorsal folium (Fig. 1d); clypeus ca. AME diameter *A. audax*
3. Males 4
Females 6
4. Pedipalpal tibia with six trichobothria *A. maculosus*
Pedipalpal tibia with less than six trichobothria 5
5. Cymbium with four slender but strong spines in a row; tegular sperm duct strongly curved (Figs. 2a, b); tegulum without distobasal processes (Fig. 2a) *A. aurioculatus*
Cymbium without conspicuous spination; tegular sperm duct slightly curved; tegulum with conical distobasal process (Figs 8a–8b) *A. mendax*
6. Opisthosoma with dorsal colour patch, framed black and white; epigynum with two large medial depressions (Figs. 9b, d) *A. mendax*
Opisthosoma without dorsal colour patch; epigynum lacks large depressions 7
7. Large species (> 5 mm); chelicerae uniformly brown *A. maculosus*
Small species (< 5 mm); chelicerae pale or slightly darkened distally *A. aurioculatus*

Australomimetes audax (Hickman 1929) new combination
(Figs. 1a–e, 10)

Mimetes audax Hickman 1929:107–110, figs. 4A–D, plate XVII; Hickman 1967:50–52, figs. 87–89, plate IX fig. 1; Roewer 1942:1021; Bonnet 1957:2917; Platnick 1997:228.

Material examined.—*Type:* AUSTRALIA: *Tasmania:* holotype ♀, Launceston (41°27'S, 147°10'E), 25 April 1928, V.V. Hickman (QVM 13:7338; Old type No. 36), examined.

Other material examined: AUSTRALIA: *Victoria:* 1 ♀, Warby Range State Park, 10 km W. of Wangaratta (36°18'S, 146°11'E), 28 July 2000, M. Scholes (QM S54173).

Etymology.—Derived from the Latin *audāx* (=bold, daring). The type-specimens were collected in webs of *Latrodectus hasselti* – the red back spider – where they were found to prey upon the offspring of the host (Hickman 1929).

Diagnosis.—Medium-sized species (carapace length 2.8–3.0 mm) distinguished from other congeners by a combination of the following characters: leg formula I IV II III, presence of a conspicuous creamy, serrated and triangular folium situated distomedially on the opisthosoma (Fig. 1d), epigynum oval; strongly sclerotized with 2 large, circular genital openings and a broad medial septum (Figs. 1a, b).

Description.—The male is unknown and the female was described by Hickman (1929, 1967). New drawings of the epigynum are provided since the originals are poor (Figs. 1a–c).

Affinities.—This species was described by Hickman (1929) within *Mimetes* based on 3 female specimens. A holotype was not designated and generic placement was not justified or discussed.

Only one female could be found in the collection of QVM; the other females are probably lost. *Mimetes audax* was not included or even mentioned in the revision of the Queensland and New South Wales fauna in which the genus *Australomimetes* was described (Heimer 1986). However, the female genital and somatic characters easily allow referral to *Australomimetes*. The species is probably a member of a group of rather robust taxa with a conspicuous whitish folium in a distomedial position on the opisthosoma (Harms & Harvey, in press). This folium is frequently present in many species from the Australian eastcoast such as *A. burnetti* Heimer 1986, *A. hartleyensis* Heimer 1986, *A. raveni* Heimer 1986 or *A. robustus* Heimer 1986 and is also very conspicuous in *A. audax*. Females of this group also share strongly sclerotized genitalia and large genital openings. Adult specimens possess a strongly maculated integument of the legs.

The position of *A. audax* within this group seems equivocal, due in part to the unusual leg formula and the reduction of the epigynal javelined scape with a broadened ectal tip, which is another prominent feature of this species group and is highly conspicuous in *A. robustus*, *A. hartleyensis* and *A. raveni* (e.g., see Heimer 1986: fig. 14). This scape shows reductive tendencies in several species (e.g. *A. mendax*) and is almost

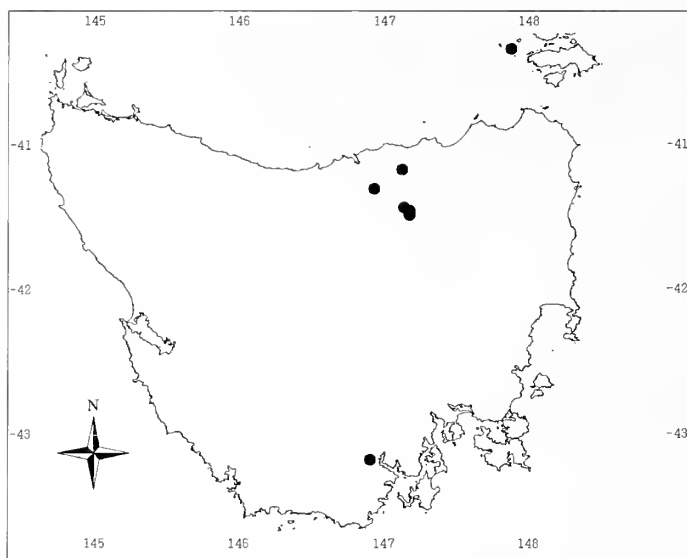


Figure 4.—Tasmanian records for *Australomimetes aurioculatus*.

completely absent in *A. audax*. *Australomimetes audax* is also very similar to *A. mendax* new species in somatic appearance and morphology and both species were probably mixed up by Hickman (1967). On the one hand, *A. audax* was included and figured in his guide to the common spiders of Tasmania although this species is rare and only the type specimens were known for a long time. On the other hand, *A. mendax* is much more common in Tasmania and it seems possible that this species was initially left undescribed because Hickman didn't recognize that there are two similar species.

Distribution.—*Australomimetes audax* is apparently rare and was only known from the three specimens described by Hickman (1929) until another female was found in Victoria. This extends the distribution range for this species to include the Australian mainland (Fig. 10).

***Australomimetes aurioculatus* (Hickman 1929)**

new combination

(Figs. 2a–f, 3, 4)

Mimetus aurioculatus Hickman 1929:110–114, figs. 6 A–C, 7 A–C; Roewer 1942:1021; Bonnet 1957:2917.

Material examined.—*Type*: AUSTRALIA: *Tasmania*: holotype ♂, Launceston (41°27'S, 147°10'E), 05 May 1929, V.V. Hickman (QVM 13:7337; Old type No. 35), examined.

Other material examined: AUSTRALIA: *Tasmania*: 1 ♀, NE. Exeter (41°18'S, 146°56'E), 30 November–9 December 2004, L.J. Boutin (QVM 13:44547); 1 ♀, 3 juveniles, WARRA Forest near Geeveston (Site C) (43°10'S, 146°54'E), 29 November 2001, L.J. Boutin (QVM 13:44549); 1 ♀, Launceston (41°26'S, 147°08'E), 1 April 1971, R. Upson (QVM 13:42367); 1 ♀, Launceston, Youngtown (41°29'S, 147°10'E), 18 May 1989, T. Boyd (QVM 13:42335); 1 ♀, Piper's River (41°10'S, 147°07'E), 6 July 1998, T. Kingston et al. (QVM 13:42164); 1 ♀, Mount Chapell Island, Bass Strait (40°20'S, 147°52'E), 29 July–7 August 1989, T. Kingston et al. (QVM 13:44550).

Etymology.—The species was named for the golden colouration of its eyes, a common feature amongst pirate spiders. The pigment, however, quickly fades in alcohol.

Diagnosis.—Small species (carapace length 1.2–1.4 mm) distinguished from other congeners by a combination of the following genitalic characters: tip of the distomedial sclerite in the male pedipalp convexe in lateral view and without additional sclerotizations, tegular sperm duct strongly curved (Fig. 2a); cymbium with four or five slender but strong spines (Figs. 2a–b).

Description.—The species was described by Hickman (1929) and redescribed by Harms & Harvey (in press). New genital drawings are provided since the original drawings are poor (Figs. 2a–f).

Variation.—The Tasmanian specimens are slightly to considerably larger than specimens from Western Australia and Queensland. Colour patterns are also more conspicuous and the cuticle is darker. Additionally, the epigynum of the Tasmanian species is often more strongly sclerotized and somewhat more conspicuous. The basal plate of the epigynum is hemiquadratic and mostly strongly pronounced. However, epigyna may vary and care must be taken in species identification because morphologically similar species exist on the Australian mainland.

Affinities.—This species clearly belongs to *Australomimetes* as it shares in the male the typical conformation of the pedipalp which includes a slender cymbium without appendages (Fig. 2a), an elongate paracymbium (Fig. 2d) and the distomedial sclerite (DMS) of the male pedipalp (Fig. 2a). Adult females possess a single cylindriciform gland spigot on each posterior spinneret which is enlarged, rotund and smooth without visible incisions (Figs 3a–b).

Within the genus *A. aurioculatus* belongs to a monophyletic group of small species with reddish and orange opisthosomal colour spots, a weak maculation of the integument of the legs and a simple male pedipalp lacking medioectal sclerites (MES). These species also share a short cheliceral paturon (Heimer 1986). This group includes species such as *A. triangulosus* Heimer, 1986, *A. miniatus* Heimer 1986 and *A. hirsutus* Heimer 1986 as well as an as yet undescribed species from New Caledonia (Harms & Harvey, in press).

Distribution and biology.—*Australomimetes aurioculatus* was originally described with no other locality than Tasmania. However, the species shows a wide distributional range and new records are established for Western Australia, New South Wales, Victoria and southern Queensland (Harms & Harvey, in press). Only the Tasmanian records are considered here (Fig. 4). The species seems to be a habitat generalist.

***Australomimetes maculosus* (Rainbow 1904)**

(Figs. 5a–f, 6a–e, 7)

Mimetus maculosus Rainbow 1904:330–332, figs. 40–42, plate XLVI figs. 5–6; Roewer 1942:1021; Bonnet 1957:2920.

Australomimetes maculosus (Rainbow): Heimer 1986:124, figs. 17–23; Platnick 1989:170.

Material examined.—*Type material*: AUSTRALIA: *New South Wales*: syntypes, 1 ♂, 6 ♀, 2 juveniles, Jenolan Caves, 29 August 1901 (AM KS5821), not examined.

Other material examined: AUSTRALIA: *Tasmania*: 1 ♀, Ulverstone, 20 Stanley Street (41°10'S, 146°11'E), 11 April 1997, A.F. Longbottom (WAM T75930); 1 ♀, Forester, 2.5 km NW of Mount Horror (41°04'S, 147°40'E), 22 March 1992, McGowan (QVM 13: 14345); 1 ♀, Exeter, West Tamar

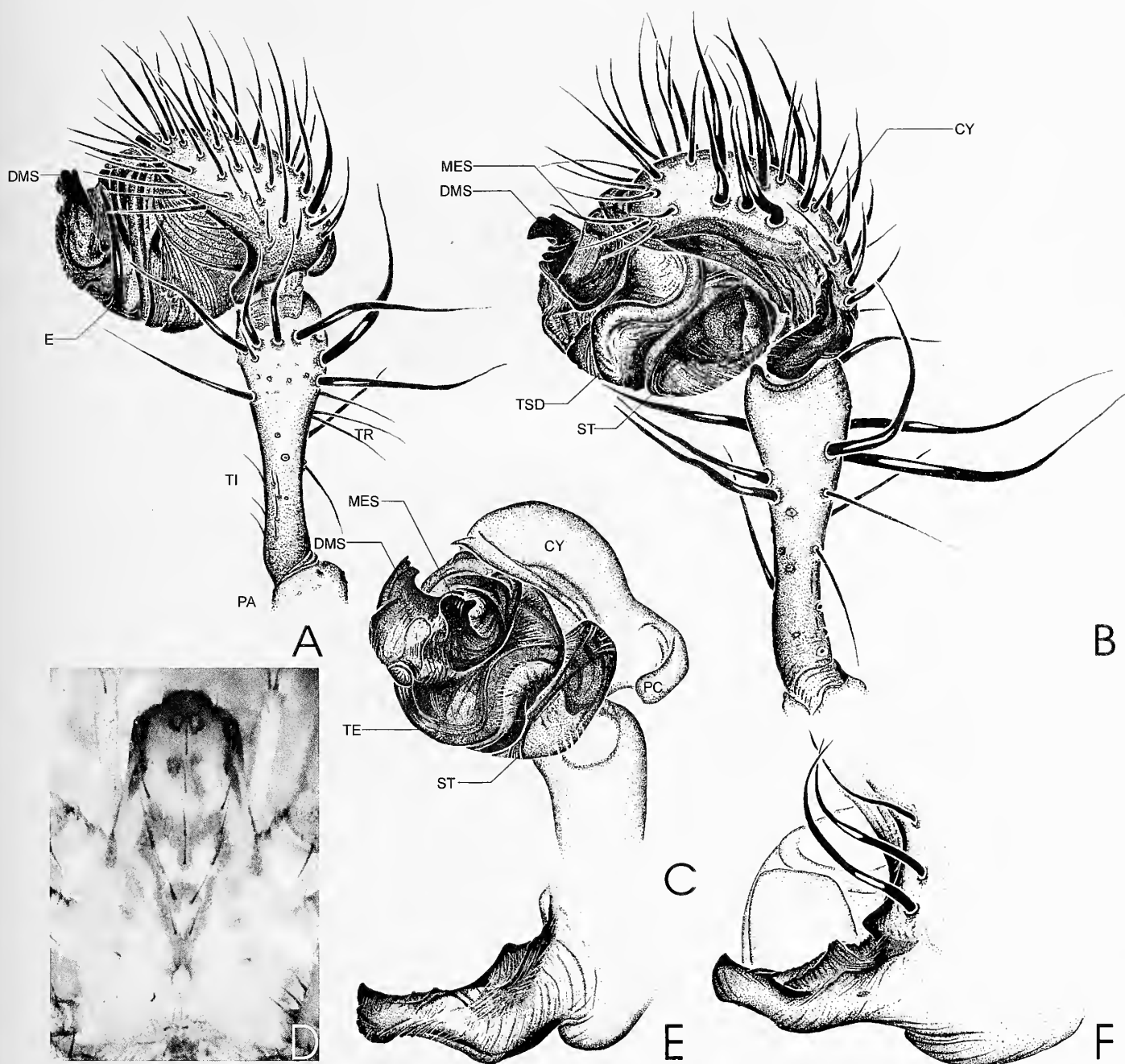


Figure 5.—*Australomimetus maculosus*. A. Male pedipalp, retrolateral view; B. Same, prolateral view (Note the presence of three or four thickened cymbial spines in a retromarginal position.); C. Same, frontolateral view. (The DMS is sickle-shaped and pointed in prolateral view); D. Female carapace, frontal view; E. Paracymbium, variation 1 from Tasmania; F. Paracymbium, variation 2 from Tasmania.

(41°16'S, 146°56'E), 9 December 1962, R.H. Green (QVM 13: 44546); 2 ♀, 1 juvenile, North Coast, Greens Beach (Tamar River) (41°05'S, 146°44'E), 31 October 1970, R.T. Green (QVM 13: 44552); 1 ♀, Launceston (41°26'S, 147°08'E), 10 November 1981, Horne (QVM 13: 42194); 1 ♀, Launceston, Norwood (41°27'S, 147°10'E), 2 May 1972, R. Upson (QVM 13: 42190); 1 ♀, Launceston, Trevallyn (51 Basin Road) (41°26'S, 147°07'E), 30 April 1988, L.R. Martin (QVM 13: 42328); 1 ♂, Launceston (41°26'S, 147°08'E), 1 April 1971, R. Upson (QVM 13: 42366); 4 ♀, 3 ♂, Launceston (41°27'S, 147°08'E), 1 February 1987, R. Raven, T. Churchill (QM

S562). *Victoria*: 1 ♂, Emerald (37°56'S, 145°27'E), 24 March 1981, M.S. Harvey (WAM T74784); 1 ♀, 1 ♂, Surrey Hills, 2 Alistair Court (37°49'26'S, 145°05'E), 15 June 1981, M.S. Harvey (WAM T74783); 1 ♀, Balwyn, 16 Fitzgerald Street (37°48'S, 145°04'E), 9 April 1981, M.S. Harvey (WAM T74785); 1 juvenile, Rye, 9 Yolland Street (38°22'S, 144°49'E), 25 December 1981, M.S. Harvey (WAM T81484); 1 ♂, Canterbury, 7 Quantock Street (37°49'S, 145°04'E), 4 April 1978, M.S. Harvey (WAM T74787); 1 penultimate ♂, Balwyn, 24 Yandilla Street (37°48'S, 145°05'E), 23 August 1981, M.S. Harvey (WAM T74786); 1 subadult ♀, Balwyn, 24

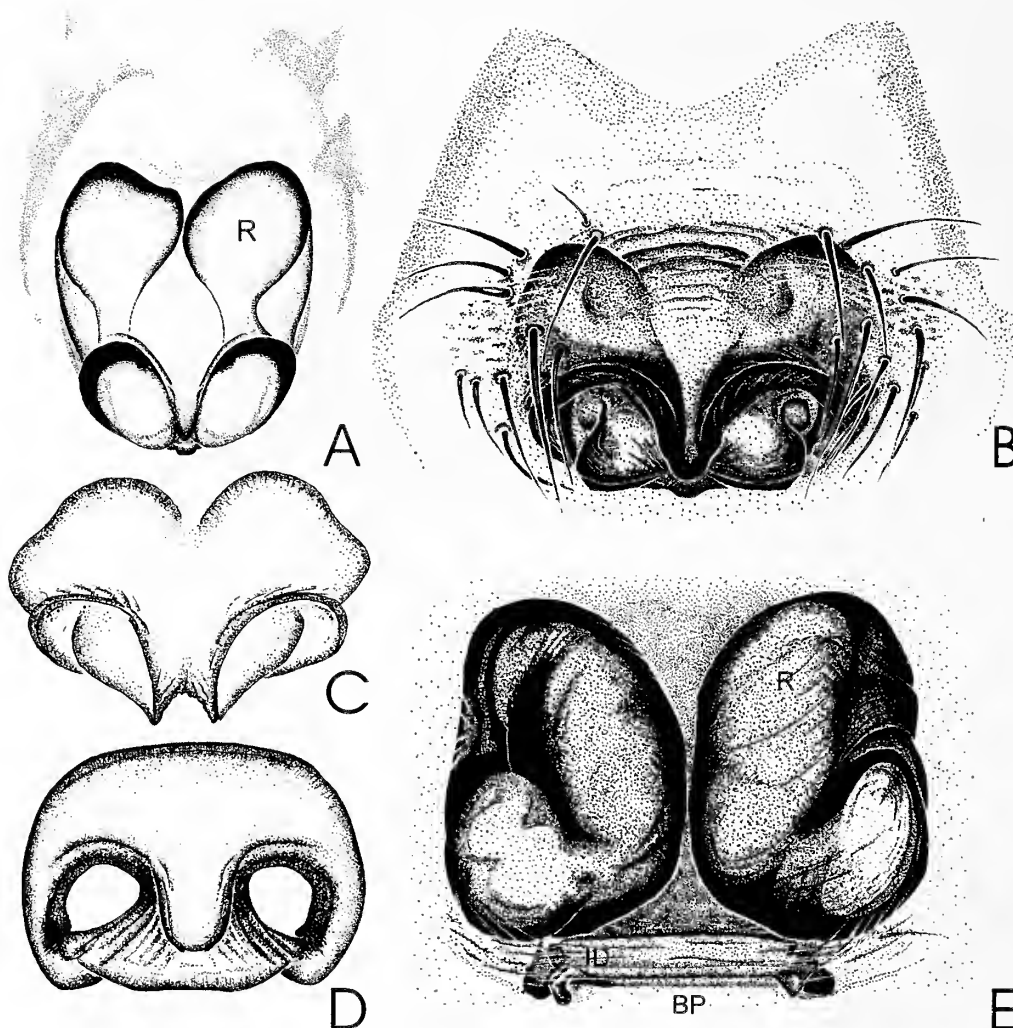
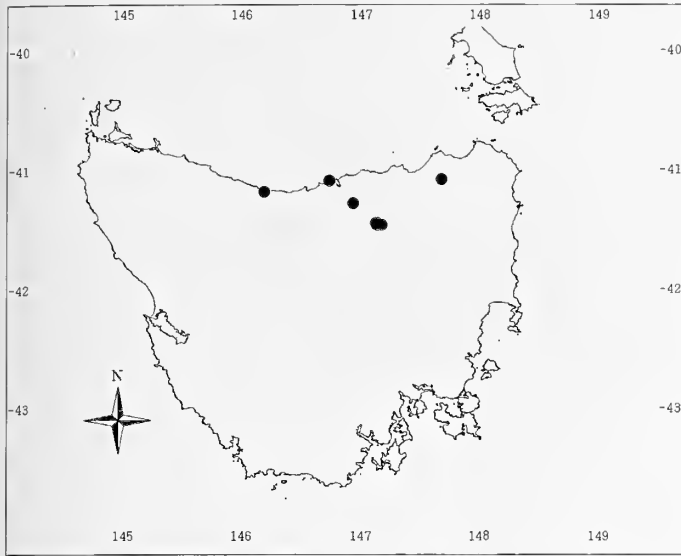


Figure 6.—*Australomimetes maculosus*, female. A. Epigynum, ventral view; variation 1 from Victoria. B–E. Same, variation 2 from Tasmania: B. Epigynum, ventral view; C. Same, anterior view; D. same, posterior view; E. Receptacula.

Yandilla Street (37°48'S, 145°04'E), 1 May 1981, M.S. Harvey (WAM T81485); 1 penultimate ♂, Knoxfield (37°53'S, 145°14'E), 21 February 1981, M.S. Harvey (WAM T81486). *Queensland*: 1 ♀, Edmonton (17°01'S, 145°44'E) 10 September 1969 (MHNG, Collection Heimer); 1 ♀, 1 ♂, Mount Goonane-man near Childers (25°26'S, 152°07'E), 3–7 October 1980 (MHNG, Collection Heimer); 2 ♂, Barron Gorge (16°52'S, 145°39'E), January 1981, R.R. Jackson (QM S32006); 1 ♀, Bellenden Ker Range (17°14'S, 145°52'E), 1–7 November 1981, Earthwatch Expedition (QM S6748); 1 ♀, 1 ♂, Redlynch, Crystal Cascades (16°53'S, 145°41'E), January 1981, R.R. Jackson (QM S32033); 1 ♀, Forty Mile Scrub, SW. of Mount Garnet (17°41'S, 145°07'E), 10–13 April 1978, R. Raven, V. Davies (QM S32011); 1 ♀, 1 ♂, Kilcoy Creek (27°00'S, 152°34'S.), 27 September 1978, K.R. McDonald (QM S32032); 1 ♀, 1 ♂, Kilcoy Creek, East branch bridge (27°00'S, 152°34'E), 8 October 1978, K.R. McDonald (QM S32034); 1 ♀, 1 juvenile ♀, Mount Halifax (19°07'S, 145°23'E), 19–21 March 1991, Monteith, Cook (QM S17950); 1 ♀, Mount Moffatt National Park, Mahogany forest (25°09'S, 147°52'E), 12 December 1987, D. Yeates (QM S32064); 1 ♂, Brooyar State Forest via Glastonbury (26°01'S, 152°23'E), Rozefelds, Sinclair (QM S32026); 2 ♀, 1 ♂, 1 juvenile ♂, Bunya National

Park (26°51'S, 151°34'E), 6 March 1976, Raven, Davies (QM S32036); 1 ♀, 3 ♂, Kroombit Tops, Dawes Range (24°23'S, 150°57'E), 9–19 December 1983, Davies, Gallon (QM S20416); 1 ♀, Kroombit Tops, Dawes Range, 45 km SSW. of Calliope (24°23'S, 150°57'E), 19 December 1983, Davies, Gallon (QM S32024); 1 ♀, Kroombit Tops, Lower Dry Creek, 45 km SSW. of Calliope (24°23'S, 150°57'E), 9–19 December 1983, Davies, Gallon (QM S32038); 1 ♂, Lamington National Park (28°15'S, 153°08'E), 10 September 1977, R. Raven (QM S32016); 1 ♂, Lamington National Park (28°15'S, 153°08'E), 24 December 1973, R. Raven (QM S32025); 2 ♀, 1 ♂, Lamington National Park, Nagarigoon (28°15'S, 153°08'E), 1–8 April 1976, R. Raven, V. Davies (QM S32070); 1 ♀, 1 ♂, Lamington National Park, Nagarigoon (28°15'S, 153°08'E), 1–8 April 1976, R. Raven, V. Davies (QM S32035); 1 ♂, Lamington Plateau (28°19'S, 153°04'E), 2 April 1975, Raven (QM S32019); 2 ♀, Lamington National Park, Binna Burra (28°11'S, 153°10'E), 5 April 1995, R. Raven (QM S30717); 1 ♀, Mount Glorious (27°23'S, 152°45'E), 1 February 1973, R. Raven (QM S32079); 1 ♀, 2 juveniles, Coolool National Park, Seary's Scrub (26°12'S, 153°01'E), 3–8 February 1976, R. Raven, V. Davies (QM S32027); 1 ♀, Upper Noosa River (26°23'S, 153°05'E), 9 August 1950, G. Filmer (QM S32037); 1



♀, Binna Burra Mountain Lodge (28°11'S, 153°10'E), 12 March 1998, P. Lawless (QM S60052); 10 ♀, North Stradbroke Island, Enterprise (27°33'S, 153°28'E), 8 January 2002 (QM S55787); 1 ♀, Hann Tableland (North End) (16°49'S, 145°11'E), 13 December 1995, Monteith, Cook, Thompson (QM S40492); 1 ♀, Mount Cotton (27°37'S, 153°13'E), 3 September–12 December 1997, G. Monteith (QM S44286); 1 ♀, 3 km S. of Mt. Spurgeon (16°27'S, 145°11'E), 19–23 November 1997, Monteith, Cook & Burwell (QM S43327); 6 juveniles, Mount Goonaneman near Childers (25°26'S, 152°07'E), 3–7 November 1980, V. Davies, R. Raven (QM S32020); 1 ♂, Top of Blackbutt Range (26°52'S, 152°11'E), 29 July–23 October 1995, G. Monteith (QM S37453); 1 ♂, Springbrook, North End (28°12'S, 153°16'E), 15 May–30 August 1997, G. Monteith (QM S43040). *New South Wales*: 1 ♂, Upper East Funnel Creek (21°34'S, 149°12'E), 15–16 November 1992, Monteith, Thompson, Cook, Janetzki (QM S26900).

Diagnosis.—Large species (carapace length 2.9–3.4 mm) distinguished from other congeners by a combination of the following somatic characters: large body size, cheliceral paturon extremely long in both sexes, more than eleven times diameter of AME and uniformly chestnut brown; absence of a serrated, whitish folium on the dorsal side of the opisthosoma. Males further distinguished from other species by the presence of 6 tibial trichobothria on the pedipalpal tibia as well as the shape of the distal sclerite of the male pedipalp (DMS) which is sickle-shaped and pointed in prolateral view (Fig. 5c).

Dimensions (mm) (WAM T74783): total length 6.22. Carapace length 3.16, width 2.17, height 0.74; AME 0.185, ALE 0.155, PME 0.180, PLE 0.145, AME-ALE 0.19, PME-
PLE 0.18, MOQ front 0.48, PER 0.96, MOQ length 0.39; clypeus 0.25; paturon 1.74. Sternum length 1.37; width 1.10. Opisthosoma length 3.06, height 1.98. Pedipalp: femur 1.49, patella 0.50, tibia 1.04, tarsus 1.03, total 4.06. Leg I: femur 6.40, patella 1.58, tibia 7.38, metatarsus 7.70, tarsus 2.58, total 25.64. Leg II: femur 5.35, patella 1.35, tibia 5.78, metatarsus 5.74, tarsus 2.02, total 20.24. Leg III: femur 3.40, patella 0.915, tibia 2.80, metatarsus 2.75, tarsus 1.27, total 11.135. Leg IV: femur 4.16, patella 0.90, tibia 3.30, metatarsus 3.16, tarsus 1.31, total 12.83.

Female (WAM T74783): As for the male except as follows:

Carapace: mediolateral spots reduced and inconspicuous, only proximal ones well defined. The 2 V-shaped patches fused. Clypeus: uniformly chestnut brown.

Sternum: with 1 distomedial brown patch which is proximomedially incised.

Legs: number of brown leg rings: leg I, femur 3, patella 1, tibia 4, metatarsus 1, tarsus 0. Leg II, femur 3, patella 1, tibia 3, metatarsus 1, tarsus 0. Leg III, femur 2, patella 0, tibia 3, metatarsus 0, tarsus 0. Leg IV, femur 1, patella 0, tibia 3, metatarsus 1, tarsus 0.

Pedipalp: patella with 3 spines, the distal spine largest; tibia with 7 trichobothria; claw serrate.

Epigynum (Figs. 6a–e): strongly sclerotized, as long as wide and with 2 large round genital openings (Fig. 6d), medially pointed but always without a scapus (Fig. 6b); posterior view reveals a median septum (Fig. 6d); receptacula slightly ovoid, genital ducts short (Fig. 6e).

Dimensions (mm) (WAM T74783): total length 6.09. Carapace length 3.22, width 2.08, height 0.74. AME 0.187, ALE 0.160, PME 0.156, PLE 0.137, AME–ALE 0.20, PME–PLE 0.28, MOQ front 0.51; PER 1.08; MOQ length 0.52; clypeus 0.35; paturon 2.04. Sternum length 1.42; width 1.11. Opisthosoma length 2.87; height 2.14. Pedipalp: femur 1.10; patella 0.50; tibia 0.94, tarsus 1.685, total 4.225. Leg I: femur 5.70, patella 1.58, tibia 6.34, metatarsus 5.74, tarsus 2.43, total 21.80. Leg II: femur 4.70, patella 1.35, tibia 4.70, metatarsus 4.43, tarsus 2.05, total 17.23. Leg III: femur 3.26, patella 0.79, tibia 2.37, metatarsus 2.50, tarsus 1.31, total 10.23. Leg IV: femur 3.89, patella 0.915, tibia 3.18, metatarsus 2.97, tarsus 1.38, total 12.335.

Variation.—Specimens from Tasmania are considerably larger than specimens collected from tropical Queensland. The female genitalia are variable and sometimes strongly sclerotized so that only 2 genital openings are visible upon a uniform brown medial plate. The medial posterior prolongation of the epigyne can also be reduced. The receptacula range from globular to slightly ovoid. A selection of common epigynal shapes is given in Figs. 6a, c–d. The paracymbium sometimes has a small ectal hook; the shape of the proximal reinforcement varies (Figs. 5d–e). However, identification of *A. maculosus* is easy by virtue of their massive size. The male pedipalp shows almost no variation and is diagnostic. The number of trichobothria on the palpal tibia also seems to be consistent.

Affinities.—*Australomimetes maculosus* is probably sister to *A. pseudomaculosus* (Harms & Harvey, in press). Males of both species share a similar shape of the distomedial sclerite (DMS) and medioectal sclerotizations (MES) of the male pedipalp, strong medial spines on the retromargin of the cymbium as well as six pedipalpal trichobothria. The species have reduced distomedial colour patterns on the opisthosoma and are the largest within the genus.

Australomimetes pseudomaculosus apparently does not occur in Tasmania. Males can be distinguished from *A. maculosus* by the presence of a medially elevated cymbium in lateral view (Heimer 1986, fig. 24). The shape of the female genitalia is also distinct from *A. maculosus* (Heimer 1986, fig. 25).

The reduction of opisthosomal colour patterns in adult specimens of *A. maculosus* and *A. pseudomaculosus* must be secondary since juveniles still possess an inconspicuous, serrated folium. The species are not closely related to *A. daviesanus* Heimer 1986 which also has the colour patterns reduced and shows a somewhat similar pedipalp (e.g. Heimer 1986, fig. 11).

Distribution and biology.—*Australomimetes maculosus* only occurs in eastern Australia, but has a wide distribution from Tasmania to tropical Queensland (Heimer 1986; Harms & Harvey, in press). It is the most common species in Australian collections. It has also been sampled from various localities in the North of Tasmania (Fig. 7). Synanthropic tendencies seem likely because it was frequently collected inside houses where it prefers dark corners and secluded places. It also occurs in caves, but such individuals do not show special morphological adaptations and the entire life cycle may not occur here. Interestingly, neither *A. maculosus* nor *A. pseudomaculosus* have been found in Western Australia. This may indicate that the species evolved in eastern Australia. The huge deserts and drylands of the Nullarbor Plain and Northern Territory may now act as effective barriers that prevent this species from a westward range extension.

Australomimetes mendax new species

(Figs. 8a–b; 9a–e, 10)

Material examined.—*Type material:* AUSTRALIA: Tasmania: holotype ♂, Wombat Hill (41°29'S, 145°26'E), 20 September 1990, R. Mesibov (QVM 13: 44524). Paratypes: AUSTRALIA: Tasmania: 2 ♀, same data as holotype (QVM 13: 44524); 1 ♀, same data as holotype except 24 September 1990 (QVM 13: 44525); 1 ♀, same data as holotype except 28 September 1990 (QVM 13: 44528), 2 ♀, same data as holotype except 19 September 1990 (QVM 13: 44526); 1 ♂, 2 ♂, Franklin River (Picnic Ground) (42°19'S, 145°47'E), 29 May 1987, T. Churchill & R. Raven (QM S29747); 1 ♂, N. of Mount Sprent via Strathgordon (42°40'S, 146°02'E), 23–25 January 1987, R. Raven, J. Gallon (QM S5696); 1 ♂, N. of Mount Sprent via Strathgordon (42°40'S, 146°02'E), 23–25 January 1987, R. Raven, J. Gallon (QM S32090).

Other material examined.—AUSTRALIA: Tasmania: 1 juvenile, Franklin River (Picnic Ground) (42°19'S, 145°47'E), 29 May 1987, Churchill & R. Raven (QM S29747); 1 ♀, Jack's Track, 27 April 1987, T. Churchill (QM S33813); 1 ♂, Cradle Mt National Park, Waldheim Forest (41°39'S, 145°57'E), 31 January–4 February 1987, T. Churchill, R. Raven (QM S5531); 1 ♀, WARRA forest near Geeveston (Site OM 5-3), 14 April 2000, D. Bashford (QVM 13: 44544); 1 ♀, WARRA Forest near Geeveston (Manuka Road) (43°10'S, 146°54'E), 5 May 2004, D. Bashford (QVM 13: 44533); 1 juvenile, Wombat Hill (41°29'S, 145°26'E), 20 September 1990, R. Mesibov (QVM 13: 44524); 1 ♀, Rattler Hill. Coll. R. Mesibov, 4 September 1990 (QVM 13: 44527); 1 ♀, Rattler Hill (41°14'S, 147°52'E), 27 August 1990, R. Mesibov (QVM 13: 44523); 2 juveniles, Magg's Mountain: Field Station (41°45'S, 146°11'E), 4 February 1980, R.H. Green (QVM 13: 42625). 1 ♀ & 2 juveniles, Russell Falls Walk (Site T 001) (42°40'S, 146°42'E), 14 January 2002, L.J. Boutin (QVM 13: 44545).

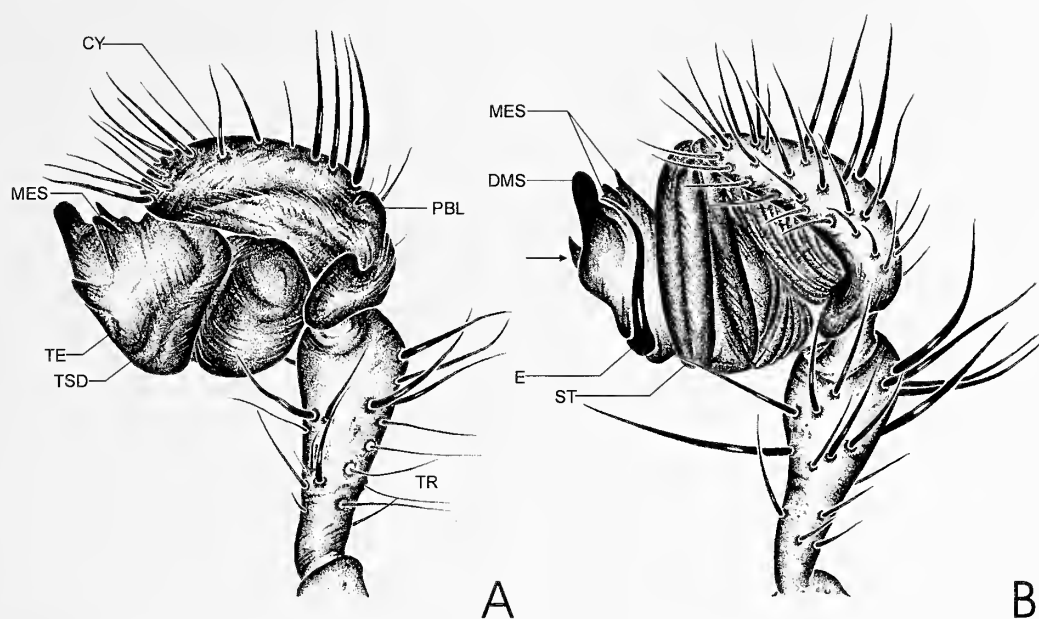


Figure 8.—*Australomimetes mendax*, male. A. Pedipalp, retrolateral view (Note the presence of five trichobothria (TR) on the tibia.); B. Same, prolateral view. Arrow points to the position of the short conical tegular process in a distobasal position. The MES consists of two cusps.

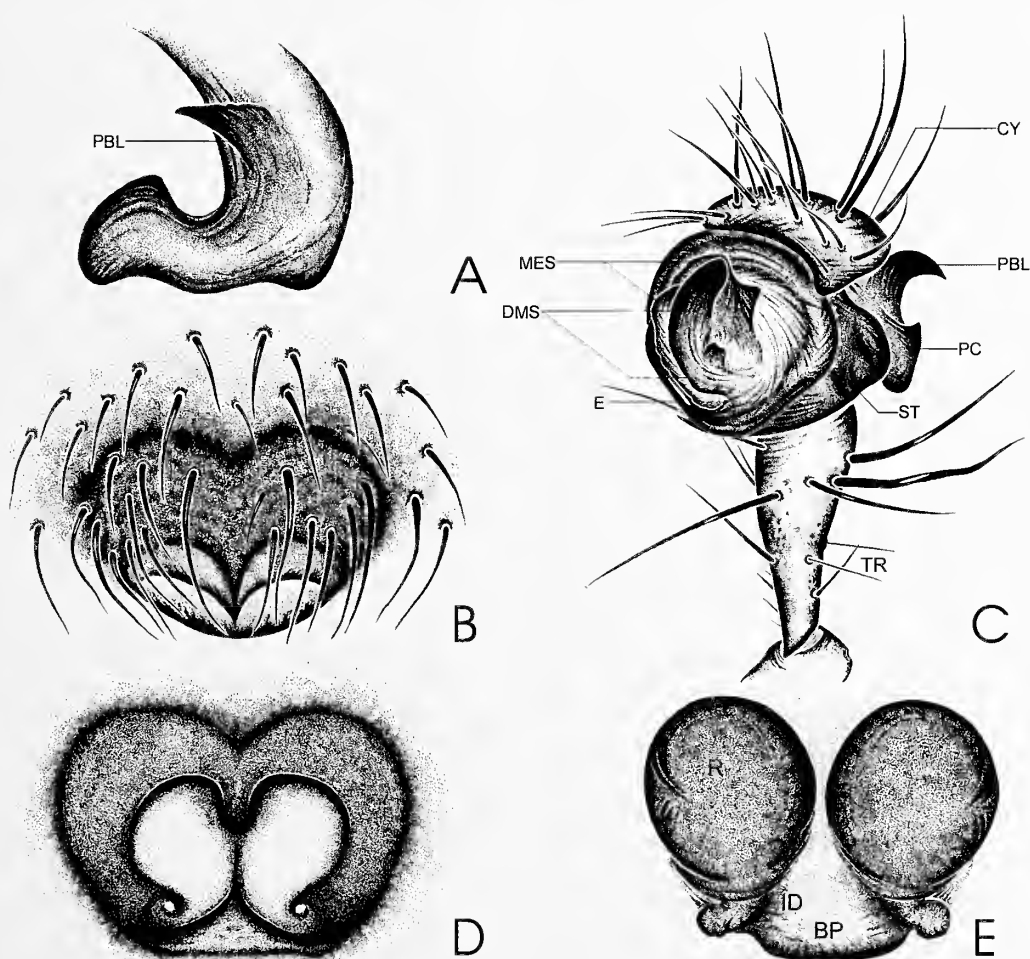


Figure 9.—*Australomimetes mendax*. A. Paracymbium, retrolateral view; B. Epigynum, ventral view; C. Male pedipalp, frontolateral view; D. Epigynum, posterior view (Note the two large medial depressions, the longitudinal median septum and the rather inconspicuous posterior genital openings.); E. Receptacula.

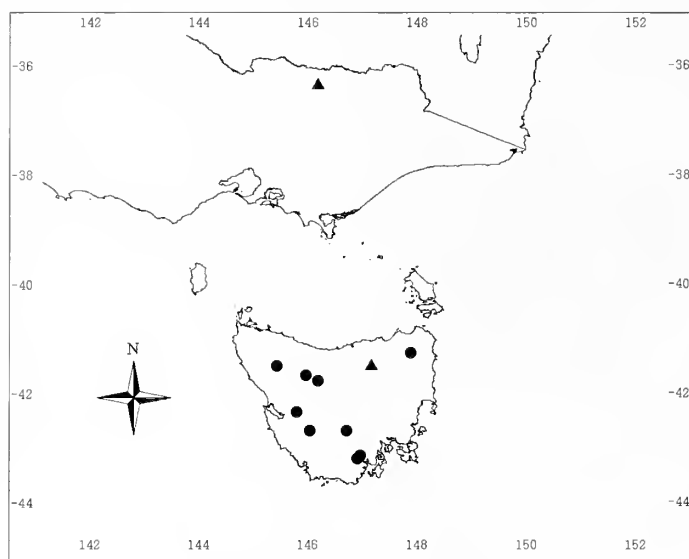


Figure 10.—Australian records for *Astralomimetus audax* (▲) and *A. mendax* (●). The latter species seems to be endemic to the island of Tasmania.

Etymology.—The epithet *mendax* (=liar) is chosen as an indication for the somatic similarities to *A. audax* which may have misled past arachnologists.

Diagnosis.—Medium-sized species (carapace length 1.9–2.6 mm) distinguished from other congeners with a creamy, serrated and triangular folium on the opisthosoma by a combination of the following genitalic characters: Distomedial sclerite (DMS) hook-shaped, elongate and with a conical distobasal process (Figs. 8a–b, arrow; also 9c), Medioectal sclerite (MES) present and with two cusps (Figs. 8a–b); two prominent patellar spines only; tegular sperm duct slightly curved (Fig. 8a). Females further distinguished from other species by the shape of the epigynum which has two large depressions and an inconspicuous medial septum (Figs. 9b–d).

Description.—*Male* (holotype, QVM 13: 44524): *Carapace*: pyriform and pale yellow; pars cephalica with brown triangular figure which consists of a sharp triangle that reaches the fovea and two lateral brown lines which are medially interspersed and rather spotted; triangle with a longitudinal pale stripe which is weakly defined; three pale colour patches between eyes and fovea, the distal one near fovea and inconspicuous; four brown spots mediolateral on each side, extended to short diagonal stripes and partly fused; margin of carapace with a further spot near base of pars cephalica; pars cephalica with three longitudinal spinal rows, mediolateral lines oblique and reaching fovea, medial line straight, all lines merging anterior to fovea; pars thoracica with two fields of 4–6 spinules in a distomedial position.

Fovea: dark brown to black, ovoid.

Eyes: LE tubercle and PME framed chestnut brown, eyes metallic golden; two spines on AME tubercle, directed anteriorly.

Clypeus: with two grey mediolateral patches and about size of AME diameter; a diagonal line of four solitary setae, the medial ones smaller than lateral ones; a further medial setum more proximal.

Chelicera: paturon proximally pale yellow with prolateral grey margins, distally darkened, about six times length of

AME; interior distal margin unidentate, promargin with peg teeth. Labium: longer than wide, yellow with lateral brown patch, distally pallid, suture brown. Endites: yellow with brown margins, distally pallid, longer than wide and converging.

Sternum: pale yellow with six lateral patches and chestnut brown; pointed and not extending between coxae IV.

Opisthosoma: with black pattern near base of petiolus, shaped like an inverted V. Laterally a black line originates which proceeds ventrally and frames the ventral side. Lateral sides with whitish foliae, another distal black line present. Distally a figure consisting of seven black spots on each side, laterally framed by whitish foliae, interrupted by a median longitudinal pale line and discontinuous. Dorsal side with whitish folium, a grey trapezoid figure at base of spinnerets and a grey patch near the tracheal spiracle present; setae yellow and strong, not dense. Spinnerets: yellow. ALS basally brown, lateral sides grey.

Legs: formula I II IV III; number of brown leg rings: leg I, femur 1, patella 1, tibia 3, metatarsus 2, tarsus 0; leg II, femur 1, patella 1, tibia 3, metatarsus 2, tarsus 0; leg III, femur 2, patella 0, tibia 3, metatarsus 2, tarsus 0; Leg IV, femur 0, patella 0, tibia 3, metatarsus 2, tarsus 0. Femur I and II with a longitudinal line of conical spinules, coxa II retrolateral with a second row of sparse spinules; claws inconspicuously serrate.

Pedipalp (Figs. 8a–b, 9c): patella with two macrosetae plus a third short one, tibia with five trichobothria in two dorsal rows (Fig. 8a); cymbium with four strong spines in a subbasal position and slightly inflected retrolaterally; paracymbium simple, elongate, broadened distally and with a scaped basal lobe (Figs. 9a, c); tegular sperm duct slightly curved (Fig. 8a); Distomedial sclerite (DMS) hook-shaped and inflected retrolaterally with a short conical process in a distobasal position, Medioectal sclerite (MES) with two cusps (Figs. 8a–b); tegular-embolic conjunction covered by an additional triangular sclerite in distobasal position, embolic tip longitudinal and terminating between medioectal sclerotizations and hooked distoectal sclerite (Fig. 8b).

Dimensions (mm) (QVM 13: 44524): total length 3.745. Carapace length 1.895, width 1.62, height 0.69; AME 0.138, ALE 0.134, PME 0.130, PLE 0.127, AME–ALE 0.06, PME–PLE 0.154, MOQ front 0.365, PER 0.71, MOQ length 0.31; clypeus 0.13; paturon 0.826. Sternum length 1.01, width 0.72. Opisthosoma length 1.85, height 1.21. Pedipalp: femur 0.77, patella 0.27, tibia 0.54, tarsus 0.653, total 2.24. Leg I: femur 3.39, patella 0.96, tibia 3.50, metatarsus 2.35, tarsus 1.42, total 11.62. Leg II: femur 2.50, patella 0.69, tibia 2.30, metatarsus 2.12, tarsus 1.15, total 8.76. Leg III: femur 1.70, patella 0.52, tibia 1.13, metatarsus 1.10, tarsus 0.77, total 5.22. Leg IV: femur 2.05, patella 0.55, tibia 1.61, metatarsus 1.40, tarsus 0.80, total 6.41.

Female (paratype, QVM 13: 44525): As for male except as follows:

Carapace: mediolateral spots on carapace not striped.

Fovea: Brown.

Chelicera: proximally yellow with two sutural brown patches, medially and distally chestnut brown; paturon about six times diameter of AME. Labium: brown, distally pale, suture black. Endites: brown, distally pale.

Sternum: with merging brown spots, forming uniform figure with six dark brown patches, a yellow patch in a medial position.

Opisthosoma: distal colour figure on opisthosoma not interspersed by colour markings and with a conspicuous outer white and an inner black frame; proximal black line framed white; ventral side with whitish foliae, hexagon of black spots present. Spinnerets: brown, ALS laterally dark brown.

Legs: number of brown leg rings: leg I, femur 1, patella 0, tibia 3, metatarsus 3, tarsus 0; leg II, femur 1, patella 0, tibia 3, metatarsus 3, tarsus 0; leg III, femur 0, patella 0, tibia 1, metatarsus 2, tarsus 0; leg IV, femur 0, patella 0, tibia 2, metatarsus 2, tarsus 0.

Pedipalp: patella with two spines, tibia with 6 trichobothria in 2 dorsal rows.

Epigynum (Figs. 9b–d): subtriangular, sclerotized and pointed; 2 large mediolateral depressions and 2 inconspicuous genital openings in posterior position to these depressions (Fig. 9d), a pointed, medial scapus (frequent in other species of the species-group) is almost absent (Fig. 9b); receptacula ovoid and genital ducts short (Fig. 9e).

Dimensions (mm) (QVM 13:44525): total length 6.08. Carapace length 2.540, width 1.87, height 0.69; AME 0.176, ALE 0.173, PME 0.123, PLE 0.1344, AME–ALE 0.10, PME–PLE 0.19, MOQ front 0.44, PER 0.90, MOQ length 0.41; clypeus 0.34; paturon 1.21; opisthosoma length 3.54, height 2.81; sternum length 1.30, width 0.945. Pedipalp: femur 0.925, patella 0.33, tibia 0.59, tarsus 0.96, total 2.81. Leg I: femur 4.30, patella 1.35, tibia 4.10, metatarsus 2.66, tarsus 1.31, total 13.72. Leg II: femur 3.30, patella 1.06, tibia 2.88, metatarsus 3.66, tarsus 1.46, total 12.36. Leg III: femur 2.23, patella 0.65, tibia 1.60, metatarsus 1.39, tarsus 1.00, total 6.87. Leg IV: femur 2.35, patella 0.65, tibia 1.65, metatarsus 1.54, tarsus 1.04, total 7.23.

Variation.—Some males have four trichobothria on the palpal tibia, whereas most males have five (Fig. 8a). The colouration is somewhat variable in males and not all colour patterns are always visible. The basal lobe of the paracymbium is sometimes shorter and not inflected.

Affinities.—This species is easily mistaken for *A. audax* since the opisthosomal colour patterns and the overall size are very similar. However, characters distinguishing the species are easily recognisable. The leg formula of *A. audax* is I IV II III; the opisthosoma has a prominent creamy whitish figure without black margins. The colour markings on the carapace are distinct. The epigynum is simple and heavily sclerotized with two simple and large genital openings. The distal margin of the cheliceral paturon is bidentate. The leg formula of *A. mendax* is - by contrast - I II IV III, the opisthosomal colour marking is less conspicuous and interspersed by black marginal serrations. The colour markings on the carapace differ and the epigynum has two large depressions and small genital openings which indicate that the two species are not even sister taxa.

Indeed, *A. mendax* is likely the sister-species of *A. sydneyensis* Heimer 1986 rather than *A. audax* (Harms & Harvey, in press). Both *A. mendax* and *A. sydneyensis* share an almost identical pedipalp structure with a short conical process in a distobasal position (Fig. 8b, arrow; “MA” in Heimer 1986, fig. 28) and a large hook-shaped distomedial

sclerite (“DMS”, Figs. 8a–b). Both species have two prominent spines on the male pedipalpal patella only whereas most other species of the genus possess three. *Australomimetus mendax* differs from *A. sydneyensis* in a number of genital features, most noticeably the shape of the tegular sperm duct which is slightly curved in *A. mendax* and strongly curved in *A. sydneyensis* (compare Fig. 8a with Heimer 1986, fig. 28 “T”). The conical distobasal process in *A. sydneyensis* inflects prolaterally, but is rather straight in *A. mendax*. The shape of the medioectal sclerite (MES) also differs. The epigynum of *A. sydneyensis* has a distal triangular velum and does not possess the two depressions (Heimer 1986, figs. 30–31). *Australomimetus sydneyensis* cannot be distinguished with confidence from *A. mendax* using somatic colour patterns alone.

Distribution.—This species has been collected all over Tasmania and is the only species which is apparently endemic to the island (Fig. 10). Since its sister-species is found in New South Wales a wider distribution range, at least for the common ancestor, must be presumed. The biology of *A. mendax* remains unknown. The species seems to be relatively common and was sampled from eucalypt and pine-wood forests around Launceston. It was also collected in the mountains which may indicate a preference for temperate, timbered habitats.

***Australomimetus tasmaniensis* (Hickman) new combination**
(Figs. 11a–c, 12a–d, 13)

Ero tasmaniensis Hickman 1929:114–116, figs. 8A–D; Heimer 1986:135–136, figs. 48–50; Roewer 1942:1019; Bonnet 1956:1799; Platnick 1989:171.

Material examined.—**Type:** AUSTRALIA: *Tasmania*: holotype ♂, Launceston (41°27'S, 147°10'E), 11 April 1905, V.V. Hickman (QVM 13:7359; Old type No. 39), examined.

Other material examined.—AUSTRALIA: *Tasmania*: 1 ♀, Frenchman's Cap track (42°05'S, 145°56'E), 24 December 1997, L.J. Boutin (QVM 13: 44554); 1 ♂, 1 juvenile, Scott's Peak, Road stop (Site T: 007) (42°59'27.1"S, 146°22'15.6"E), 18 January 2002, L.J. Boutin (QVM 13: 44551); 1 ♀, Picton Valley (site WR9) (43°13'S, 146°40'E), 3 December 1994, K. Michaels (QVM 13: 44558); 1 ♂, Picton Valley (Site Tomalah Creek, WR9) (43°13'S, 146°41'E), 15 July 1994, K. Michaels (QVM 13: 44557); 1 ♂, WARRA Forestry, site near Geeveston at Manuka Road (43°07'S, 146°67'E), 25 February 2004, R. Bashford (QVM 13: 44532); 1 ♀, Lake St Clair, Pump House Point PF 08 (42°07'S, 146°10'E), 11 March 1995, T. Kingston et al. (QVM 13: 23812); 3 ♀, Old Cham Dam Area (41°06'S, 148°05'E), 22 June 1995, M. McCornick (QVM 13: 44548); 1 ♀, Blue Tier Site (BTWHSB2) (41°19'43"S, 148°07'81"E), i.2001, M. MacDonald (QVM 13: 44555); 1 ♀, Blue Tier Site (BTWHSB2) (41°19'43"S, 148°07'81"E), i.2001, M. MacDonald (QVM 13: 44555); 1 ♀, Pipers River (41°05'S, 147°04'E), 6 July 1993, T. Kingston et al. (QVM 13: 42165); 1 ♂, WARRA Forestry, Site near Geeveston No. 282 (43°07'S, 146°65'E), 22 April 1998, D. Bashford (QVM 13: 44537); 1 ♀, 1 ♂, Picton Valley (Site WR93A) (43°13'S, 146°41'E), 16 April 1994, K. Michaels (QVM 13: 44556); 1 ♂, WARRA Forest near Geeveston (Site: 282) (43°10'S, 146°54'E), 22 April 1998, D. Bashford (QVM 13: 44537); 1 ♀, WARRA Forest near Geeveston (Site: 06) (43°10'S, 146°54'E), 16 March 2000, D.

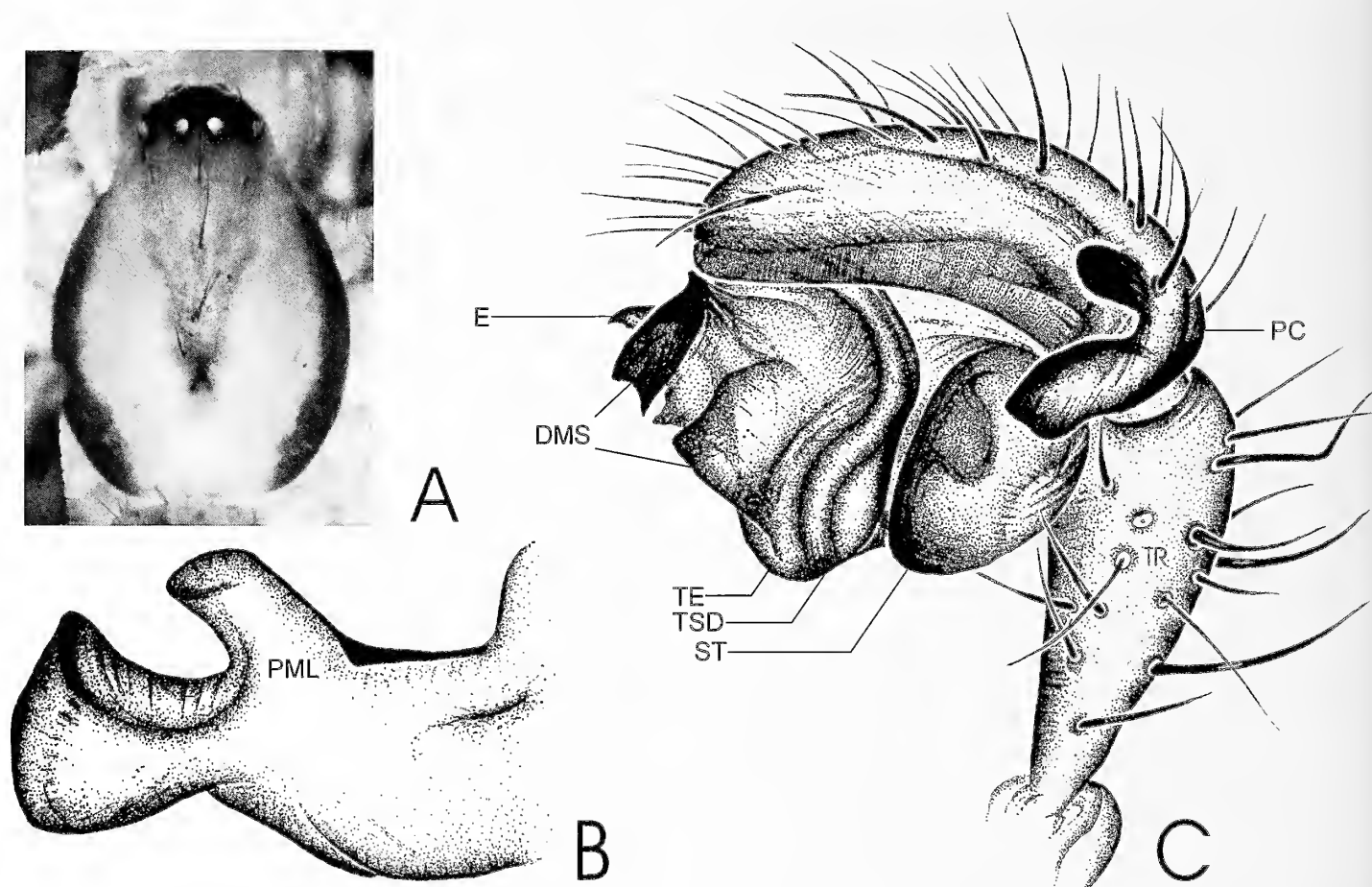


Figure 11.—*Australomimetes tasmaniensis*. A. Carapace, female, frontal view; B. Paracymbium, inner frontal view (Note the paracymbial medial lobe (PML) is almost hemi-quadratic.); C. Pedipalp, male, retrolateral view (Note the absence of a medioectal sclerite (MES) on the tegulum.).

Bashford (QVM 13: 44534); 1 ♀, WARRA Forest (43°10'S, 146°54'E), December 1997, D. Bashford (QVM 13: 44536); 1 ♀, WARRA Forest (43°10'S, 146°54'E), 14 January 1998, D. Bashford (QVM 13: 44541); 1 ♀, Old Cham Dam Area (41°06'S, 148°05'E), December 2000, M. McCormick (QVM 13: 44549); 1 ♀, Old Cham Dam Area (41°06'S, 148°05'E), December 2000, M. McCormick (QVM: 13:44549); 1 ♀, WARRA Forest (43°10'S, 146°54'E), 11 August 2000, D. Bashford (QVM 13: 44530); 1 ♂, WARRA Forest near Geeveston (43°10'S, 146°54'E), 2 August 2000, D. Bashford (QVM 13: 44539); 1 ♂, WARRA Forest (Site 518) (43°10'S, 146°54'E), 25 July 2000, D. Bashford (QVM 13: 44535); 1 ♂, 5 km ENE. of McPartlan Pass, 22 January 2002, D. Driscoll (QVM: 13:44553); 1 ♂, WARRA Forest (43°10'S, 146°54'E), 12 May 2000, D. Bashford (QVM 13: 44538); 1 ♀, WARRA forest (Site: 70) (43°10'S, 146°54'E), 12 February 1998 (QVM 13: 44531); 1 ♂, WARRA forest (Site: 226) (43°10'S, 146°54'E), 14 January 1998, D. Bashford (QM 13: 44540).

Etymology.—The specific epithet refers to the location of the type series, the island of Tasmania.

Diagnosis.—Small species (carapace length 1.0–1.6 mm) distinguished from other congeners by the combination of the following somatic characters: robust appearance and relatively short legs, unusual leg formula of I IV II III, presence of pronounced broad leg rings, carapace framed by a broad,

darkened lateral line and ovoid rather than pyriform (Fig. 11a), clypeus higher than diameter of AME tubercle. Males further distinguished from other species by the presence of a single spine on the pedipalpal patella as well as the presence of only three trichobothria on the pedipalpal tibia (Fig. 11c).

Description.—This species was described by Hickman (1929) and redescribed by Heimer (1986) and Harms & Harvey (in press). We provide new genital drawings for the Tasmanian population since the original drawings by Hickman (1929) and Heimer (1986) are poor. The female genitalia are presented in their known variations.

Variation.—Specimens from Tasmania are dusky in coloration and the opisthosoma can be almost completely dark. The epigynum of Tasmanian species is relatively broad and the basal plate hemiquadratic and seldom tipped (Fig. 12a). The receptacula frequently possess a huge basal lobe and the receptaculum looks somewhat tripartite (Fig. 12c).

Affinities.—Based on striking similarities in the male pedipalpal structure such as the presence of a distomedial sclerite (DMS; Fig. 11c) but also in the female genitalia, this species clearly belongs to *Australomimetes* rather than *Ero*. Also, lines of short conical spines on femora I and II – hypothesized to be autapomorphic for the derived Mimetinae excluding *Ero* (Harms & Harvey, in prep.) – are clearly present

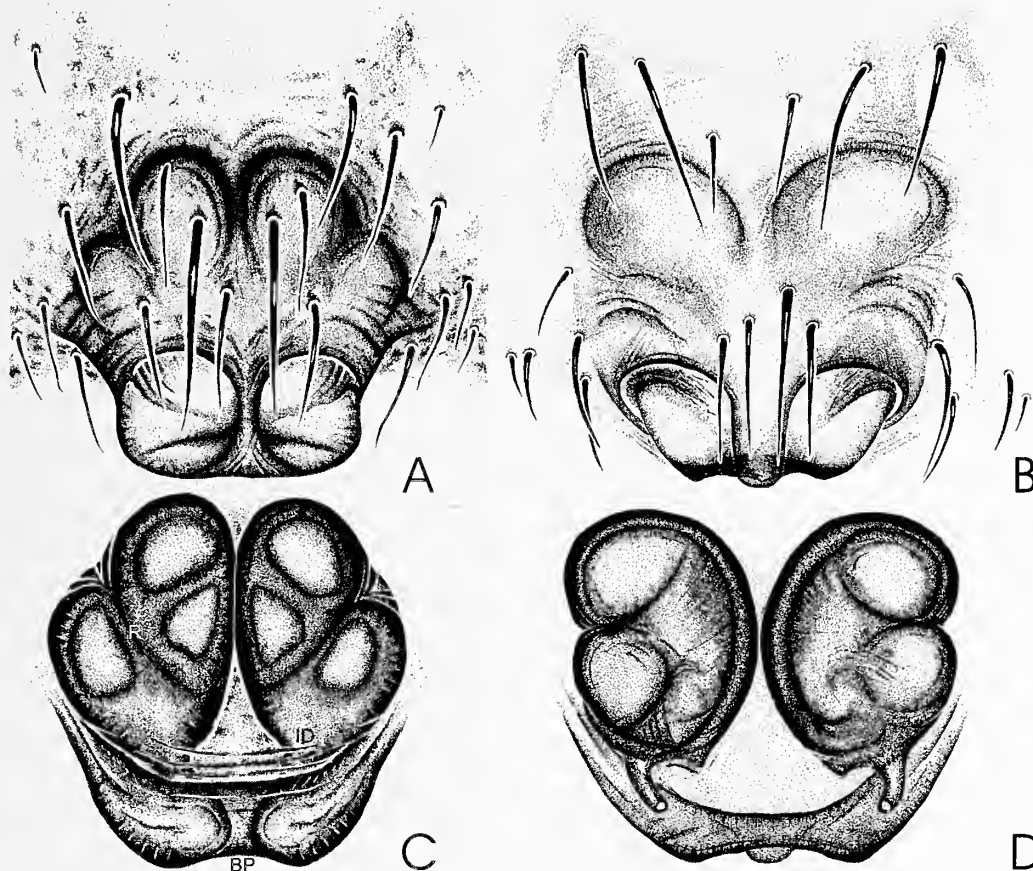


Figure 12.—*Australomimetes tasmaniensis*, female. A. Epigynum, variation 1 from Tasmania; B. Epigynum, variation 2 from Western Australia; C. Receptacula, variation 1 from Tasmania, view slightly posterior; D. Receptacula, variation 2 from Western Australia.

(see also Hickman 1929). An undescribed sister-species from Western Australia which is clearly a member of *Australomimetes* will be described in an upcoming paper that addresses the pirate spiders from Western Australia (Harms & Harvey, in press). The affinities, however, of these two species within the genus remain somewhat enigmatic and some unusual

morphological features, such as the high clypeus, leg formula of I IV II III and robust appearance due to its relatively short legs, might be related to its preference for cursorial habitats.

Distribution.—This species is widely distributed over much of Tasmania through to tropical Queensland, Western Australia and the Northern Territory. It was also found in New South Wales (Heimer 1986). The map shown here (Fig. 13) considers Tasmanian records only.

DISCUSSION

Interrelationships of Tasmanian Mimetidae.—Although a cladistic analysis is required to delimit monophyletic species-groups within the genus *Australomimetes*, our findings imply that the Tasmanian species are not monophyletic as revealed by peculiar and multiple genitalic and somatic disparities. *Australomimetes aurioculatus* probably belongs to a monophyletic group of rather small species in which the distomedial sclerite (DMS) of the male pedipalp is simple and the medioectal sclerite (MES) mostly absent. The opisthosomal cuticle is often adorned with reddish or orange colour spots and the setation of the opisthosomal integument is rather weak. The majority of species with a similar somatic and genitalic appearance are found in tropical Queensland, although two species are also known from Western Australia (Harms & Harvey, in press). *Australomimetes tasmaniensis*—although of similar size—does not belong to this group and a similar species from Western Australia will be described

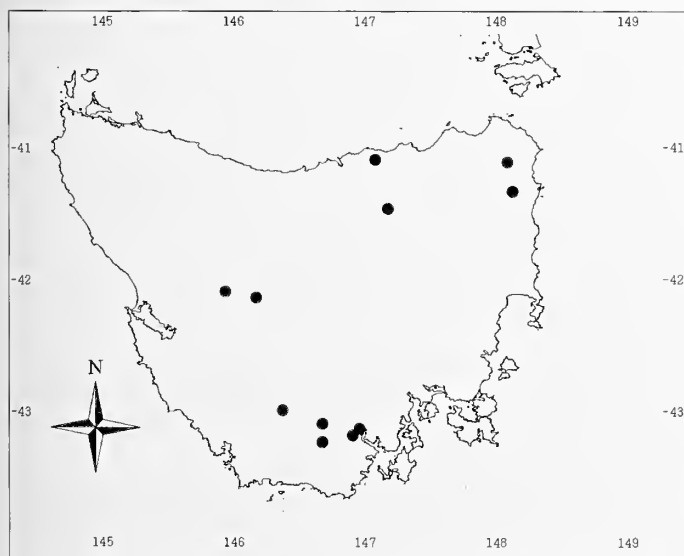


Figure 13.—Tasmanian records for *Australomimetes tasmaniensis*.

elsewhere. *Australomimetes mendax* and *A. audax* both belong to a third group of rather robust species which share a conspicuous whitish folium on the dorsal opisthosomal cuticle (Fig. 1d), strong rows of conical spinules on femora I and II, and - in most species - a javelined scape on the female epigynum (e.g. Heimer 1986, figs. 13, 14, 30). A detailed study of material deposited in the Queensland Museum reveals that most of these species are distributed in tropical Queensland and that the presumed species-group is subject to ongoing allopatric speciation and radiation. Due to the striking interspecific similarities but intraspecific variability in genital morphology this group may present a significant taxonomic challenge.

Biogeography.—Four of the five Tasmanian species are also distributed on the Australian mainland (Harms & Harvey, in press), suggesting that the Bass Strait does not effectively prevent trans-oceanic dispersal in both directions or, alternatively, that the geological isolation of Tasmania which has lasted for 12,000 to 13,000 years (Sanmartin & Ronquist 2004; Brown & Lomolino 1998) was not sufficient to allow the formation of new species. Neither possibility can be definitively ruled out, but from the extremely wide distribution ranges of some species - extending from the east to the west coast of the Australian mainland - it would appear that at least the occurrences of *A. aurioculatus* and *A. tasmaniensis* in Tasmania are a secluded relic of a previously cohesive distribution that extended from northern Queensland to southern Western Australia. The Tasmanian populations might have become isolated when Bass and Banks Strait opened, leading to the formation of Tasmania as an island, and morphological differentiation of the Tasmanian populations.

The collection records of *A. mendax* and *A. sydneyensis* are interesting in this matter. Of all five Tasmanian mimetid species, only *A. mendax* is currently endemic to Tasmania with its putative sister-species *A. sydneyensis* from New South Wales found about 900 km apart. The close morphological similarities between both species suggest a common ancestor for both species and rather recent allopatric speciation events. It would be of interest to test the affinities of both species on a genetic level, using a molecular clock in order to estimate the time that the two species diverged and the possible divergence date.

Variation.—All species described and illustrated throughout this paper normally exhibit a certain amount of variability in the structures of the male and female genitalia. Specimens of a single species usually differ slightly from one another in the shape and sclerotization of the epigyne, length of the male pedipalpal tibia, shape of the paracymbium, DMS and MES but also in the colouration markings of the opisthosomal cuticle. These variations are normal and some drawings on variability are given above. Beside these individual variations, we also found some general modifications which interestingly appear to be relatively stable amongst the Tasmanian populations of a single species and set them apart from their counterparts from the Australian mainland. Tasmanian specimens often differ from mainland Australian specimens in terms of body size, cuticle sclerotization and shape of the genitalia. Female Tasmanian specimens often have more strongly sclerotized receptacula and broader epigyna when compared to specimens of the same species from the

Australian mainland (e.g. compare Figs 12a–b or 12c–d). The body cuticle of both sexes is often heavily sclerotized, giving the species a darker appearance in general. Specimens of *A. maculosus* and *A. tasmaniensis* are also significantly larger than their counterparts from Queensland or New South Wales. Adult specimens of *A. maculosus* were found to be about double the size of specimens collected in tropical Queensland. This might all be due to longer generation cycles and slower body growth due to lower average temperatures in temperate Tasmania compared to subtropical or tropical mainland Australia; something which also holds true for the New Zealand species.

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LITERATURE CITED

- Barrion, A.T. & J.A. Litsinger. 1995. *Riceland Spiders of South and Southeast Asia*. CAB International, Wallingford, UK. 736 pp.
- Brown, J.H. & M.V. Lomolino. 1998. *Biogeography*. Sinauer Associates, Sunderland, Massachusetts. 560 pp.
- Bryant, E.B. 1935. Some new and little known species of New Zealand spiders. *Records of the Canterbury Museum* 4:71–94.
- Coddington, J.A., G. Giribet, M.S. Harvey, L. Prendini & D.E. Walter. 2004. Arachida. Pp. 296–318. *In* *Assembling the Tree of Life*. (J. Cracraft & M.J. Donoghue, eds.). Oxford University Press, New York.
- Cutler, B. 1972. Notes on the biology of *Mimetes puritanus* Chamberlin (Araneae: Mimetidae). *American Midland Naturalist* 87:554–555.
- Forster, R.R. & N.I. Platnick. 1984. A review of the archaoid spiders and their relatives, with notes on the limits of the superfamily Palpimanoidea (Arachnida, Araneae). *Bulletin of the American Museum of Natural History* 178(1):1–106.
- Forster, R.R. & L.M. Forster. 1999. *Spiders of New Zealand and their Worldwide Kin*. University of Otago Press, Dunedin, New Zealand.
- Griswold, C.E., M.J. Ramírez, J.A. Coddington & N.I. Platnick. 2005. *Atlas of phylogenetic data for entelegyne spiders (Araneae:*

- Araneomorphae: Entelegynae) with comments on their phylogeny. *Proceedings of the California Academy of Sciences* 56(2):1–324.
- Harms, D. (in press). *Australomimetes kuutneri* sp. nov., the first record of a pirate spider from Indonesia (Arachnida: Araneae: Mimetidae). *Zoosystematics and Evolution*.
- Harms, D. & M.S. Harvey. (in press). Systematics and phylogeny of the Australian pirate spiders (Araneae, Mimetidae) with a revision of the Western Australian fauna. *Invertebrate Systematics*.
- Heimer, S. 1986. Notes on the spider family Mimetidae with description of a new genus from Australia (Arachnida, Araneae). *Entomologische Abhandlungen Staatliches Museum für Tierkunde Dresden* 49:113–137.
- Heimer, S. 1989. Some new mimetid spiders from North Queensland, Australia (Arachnida, Araneae, Mimetidae). *Memoirs of the Queensland Museum* 27:433–435.
- Hickman, V.V. 1929. Studies in Tasmanian spiders. Part III. Papers and Proceedings of the Royal Society of Tasmania 1928:96–118.
- Hickman, V.V. 1967. Some Common Spiders of Tasmania. Tasmanian Museum Art Gallery, Hobart, Australia. 112 pp.
- Jackson, R.R. & M.E.A. Whitehouse. 1986. The biology of New Zealand and Queensland pirate spiders (Araneae, Mimetidae): aggressive mimicry, araneophagy and prey specialization. *Journal of Zoology London (A)* 210:279–303.
- Kloock, C.T. 2001. Diet and insectivory in the araneophagic spider *Mimetes notius* (Araneae: Mimetidae). *American Midland Naturalist* 146:424–428.
- Mascord, R. 1970. *Australian Spiders in Colour*. Reed Books Pty Ltd, Balgowlah, Australia. 112 pp.
- Paquin, P. & N. Dupérré. 2003. Guide d'identification des Araignées (Araneae) du Québec. *Fabriques, Supplément* 11:1–251.
- Pickard-Cambridge, O. 1879. On some new and rare spiders from New Zealand, with characters of four new genera. *Proceedings of the Zoological Society of London* 1879:681–703.
- Platnick, N.I. 2008. The World Spider Catalog, Version 9.0. American Museum of Natural History, New York. Online at <http://research.amnh.org/entomology/spiders/catalog/index.html>.
- Platnick, N.I. & M.U. Shadab. 1993. A review of the pirate spiders (Araneae, Mimetidae) of Chile. *American Museum Novitates* 3074:1–30.
- Rainbow, W.J. 1904. Studies in Australian Araneidae No. 3. *Records of the Australian Museum* 5:326–336.
- Sanmartin, I. & F. Ronquist. 2004. Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology* 53:216–243.
- Schütt, K. 2000. The limits of the Araneoidea (Arachnida: Araneae). *Australian Journal of Zoology* 48:135–153.
- Schütt, K. 2003. The limits and phylogeny of the Araneoidea (Arachnida: Araneae). Ph.D. dissertation. Humboldt-Universität, Berlin. 152 pp.
- Simon, E. 1892–1895. *Histoire Naturelle des Araignées*, Vol. I:940–948. Librairie Encyclopédique de Roret, Paris.
- Thaler, K., A. van Harten & B. Knoflach. 2004. Pirate spiders of the genus *Ero* C.L. Koch from southern Europe, Yemen, and Ivory Coast, with two new species (Arachnida, Araneae, Mimetidae). *Denisia* 13:359–368.
- Urquhart, A.T. 1891. On new species of Araneae. *Transactions and Proceedings of the New Zealand Institute* 23:128–189.
- Wiehle, H. 1953. Spinnentiere oder Arachnoidea (Araneae) IX: Orthognatha – Cribellatae – Haplogynae – Entelegynae. *Tierwelt Deutschlands* 42:1–150.

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Redescription of *Rhopalurus abudi* (Scorpiones, Buthidae), with first description of the male and first record from mainland Hispaniola

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Abstract. *Rhopalurus abudi* Armas & Marcano Fondeur 1987 was originally described on the basis of a single female specimen from Isla Saona, La Romana Province, off the southeast coast of the Dominican Republic. The species is redescribed here based on a series of new specimens including 19 adult males and 14 adult females collected at two nearby localities on the eastern side of Parque Nacional del Este, La Altagracia Province, southeastern Dominican Republic. These specimens represent the first records of *R. abudi* on mainland Hispaniola and the first male specimens of the species to be collected.

Keywords: Alacran, Caribbean, Dominican Republic, Parque Nacional del Este, taxonomy, biogeography

The buthid scorpion genus *Rhopalurus* Thorell 1876 comprises 18 species and three subspecies (one nominotypical) of relatively large, lapidicolous (Prendini 2001a) scorpions with a discontinuous distribution in the Greater Antilles (Cuba and Hispaniola) and northern South America (Brazil, Colombia, Guyana, and Venezuela) (Appendix 1). These scorpions are unique in possessing the ability to stridulate audibly by scraping nodules and/or ridges on the dorsal surfaces of their pectines against granules on the ventral surfaces of mesosomal sternite III, a remarkable behavior that presumably functions to deter would-be predators (Pocock 1904; Lourenço & Cloudsley-Thompson 1995; Armas 2001; Lourenço 2007). Lourenço (1986) considered the stridulation organ to be synapomorphic for *Rhopalurus*, a hypothesis that has yet to be tested cladistically.

The taxonomic distinction between *Rhopalurus* and another New World buthid scorpion genus, *Centruroides* Marx 1890, distributed from the southwestern USA throughout Mexico, Central America, the Greater and Lesser Antilles, to northern South America (Colombia, Ecuador, and Venezuela), remains unclear. The two genera are separated primarily according to the presence, in *Rhopalurus*, of the stridulation organ on opposing surfaces of sternite III and pectines, which is absent in *Centruroides* (Lourenço 1979; Sissom 1990). The stridulation organ is variably developed within the genus, however, and the species of *Rhopalurus* form a rather heterogeneous assemblage in other respects. Evidence from ovariuterine morphology (Volschenk et al. 2008) and DNA sequences (L.A. Esposito, E.S. Volschenk & L. Prendini, in prep.) suggests that *Rhopalurus* may be paraphyletic with respect to *Centruroides*.

Rhopalurus was last revised by Lourenço (1982). Numerous changes to its composition have been made since then (Lourenço 1984, 1986, 2002, 2007; Armas & Marcano Fondeur 1987; Lourenço & Pinto-da-Rocha 1997; Armas 1999; Lourenço et al. 2004; Lenarducci et al. 2005; Teruel 2006; Teruel & Armas 2006; Teruel & Roncallo 2008; Teruel & Tietz 2008; Lourenço 2008). These include the description of 10 new species, one of which was subsequently synonymized, and two new subspecies; the resurrection of a species previously placed in synonymy; the elevation of a subspecies to species rank; the resurrection of a monotypic genus,

Physoctonus Mello-Leitão 1934, to accommodate a species once placed in *Rhopalurus*; and the creation of another monotypic genus, *Troglorhopalurus* Lourenço et al. 2004, to accommodate a new troglomorphic species. The validity of *Physoctonus* and *Troglorhopalurus* is presently unclear. The systematics of *Rhopalurus* and related genera warrants reinvestigation, including detailed morphological revision and rigorous cladistic analysis based on morphological and molecular data.

Three species of *Rhopalurus* are endemic to Hispaniola (Armas 1999, 2001; Fet & Lowe 2000; Teruel 2005, 2006; Fig. 1). *Rhopalurus abudi* Armas & Marcano Fondeur 1987 (Figs. 2, 5A, B, 6A, 7A, 8, 11) and *Rhopalurus bonettii* Armas 1999 (Figs. 3, 5C, D, 6B, 7B, 9) are endemic to the Dominican Republic (DR), whereas *Rhopalurus princeps* (Karsch 1879) (Figs. 4, 5E, F, 6C, 7C, 10) also occurs in Haiti. *Rhopalurus abudi*, described on the basis of a single female specimen from Isla Saona, La Romana Province, off the southeast coast of the DR, is the least known of the three species and among the least known species in the genus. No new records of this species have been reported in the literature since the original description (Armas & Marcano Fondeur 1987; Armas et al. 1999; Teruel 2005, 2006). Lourenço & Pinto-da-Rocha (1997:181) suggested that it may be a junior synonym of *R. princeps* (see also Fet & Lowe 2000:217).

In July 2004, an expedition to collect arachnids in the DR was conducted by EV and JH. During the course of that expedition, a series of new specimens of *R. abudi*, including 19 adult males and 14 adult females, was collected in humid coastal forest at two nearby localities on the eastern side of Parque Nacional del Este, La Altagracia Province, southeastern DR. These specimens represent the first records of *R. abudi* on mainland Hispaniola, the first male specimens of the species to be collected, and the first records of a *Rhopalurus* species from a humid coastal forest habitat. On the basis of this new material, we provide a detailed redescription of *R. abudi*, including a comparison with the other two species of *Rhopalurus* endemic to Hispaniola.

METHODS

Specimens were collected using ultraviolet (UV) light detection at night or by rolling limestone boulders during

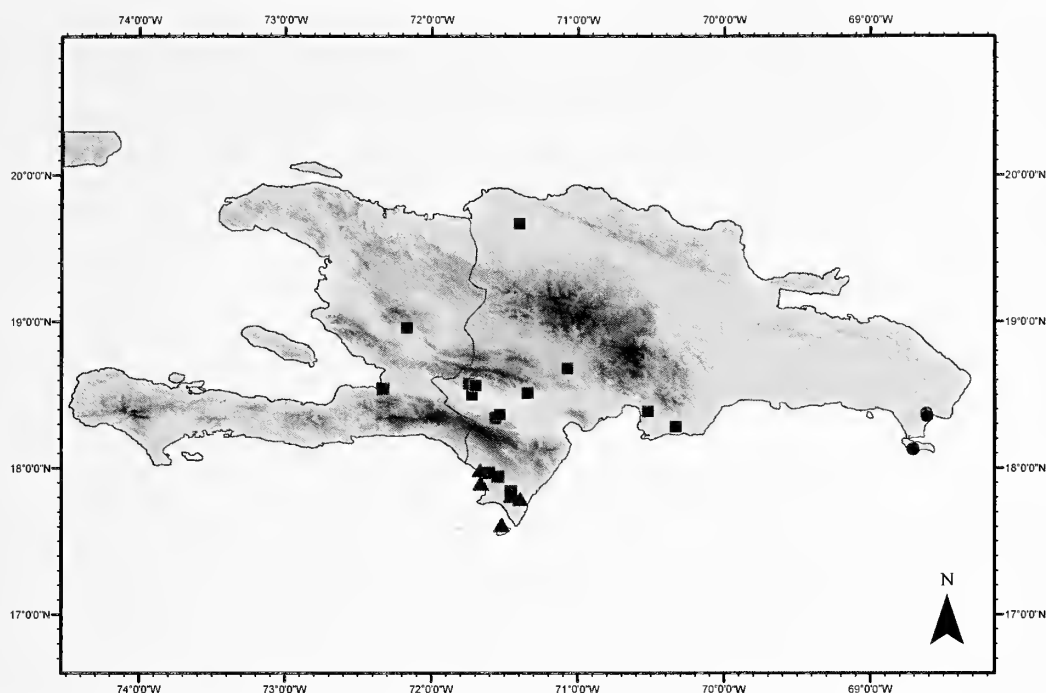


Figure 1.—Map of Hispaniola showing new and published locality records for *Rhopalurus abudi* Armas & Marcano Fondeur 1987 (circles), *Rhopalurus bonettii* Armas 1999 (triangles) and *Rhopalurus princeps* (Karsch 1879) (squares).

the day. Geographical coordinates and elevation were recorded with a portable Garmin GPS V Personal Navigator device, using the WGS84 datum. Most specimens were preserved in the field in 75% ethanol. One specimen from each locality was preserved in 95% ethanol for future DNA isolation.

Specimens were examined using a Nikon SMZ1500 dissection stereomicroscope. Hemispermatothores were dissected following the method described by Prendini et al. (2006) and the soft paraxial tissues dissected away from the capsule area using minuten entomology pins prior to examination in 75% ethanol. Specimens for which tissue could not be completely removed from the capsule area were dehydrated in ethanol (80% for 10 min, 95% for 10 min), followed by isopropanol (100% for 10 min), and then cleared in clove oil for ~ 20 min. Specimens were measured using Mitutoyo® digital calipers and an ocular micrometer. Ultraviolet fluorescence and conventional light photomicrographs were prepared, following a modified version of the method outlined by Volschenk (2005), using a Microptics™ ML-1000 digital imaging system, and the digital images subsequently edited and prepared into plates with the aid of Adobe Photoshop and Corel Draw.

Specimens of *R. abudi*, other species of *Rhopalurus* and related taxa studied for comparison (Appendix 2) are deposited in the following collections: American Museum of Natural History (AMNH), New York, USA, incorporating the Alexis Harington (AH) Collection; Natur-Museum Senckenberg, Frankfurt (SMF), Germany; Zoologisches Museum der Humboldt-Universität, Berlin (ZMB), Germany; Zoologisches Museum der Universität Hamburg (ZMH), Germany. Reference numbers (ESV and LP), provided on labels with the specimens, correspond to entries in the specimen databases of the author with the corresponding initials.

General anatomy follows Hjelle (1990) and Sissom (1990), trichobothria follows Vachon (1974), carination follows Prendini (2001b), and hemispermatothore follows reinterpretation of the character system in Buthidae, to be described fully elsewhere. Ovariuterine anatomy follows Volschenk et al. (2008). Measurements follow Stahnke (1970), Lamoral (1979), and Prendini (2001b).

TAXONOMY

Family Buthidae C.L. Koch 1837

Genus *Rhopalurus* Thorell 1876

Rhopalurus abudi Armas & Marcano Fondeur 1987
(Figs. 2, 5A, B, 6A, 7A, 8, 11)

Rhopalurus abudi Armas & Marcano Fondeur 1987:19–20, fig. 4, pl. II, tab. 10; Rudloff 1994:9; Lourenço & Pinto-da-Rocha 1997:181; Kovařík 1998:118; Armas 1999:127; Armas et al. 1999:30–32; Armas 2001:246, tab. 1; Fet & Lowe 2000:217; Fet et al. 2003:3, tab. 1; Teruel 2005:165; Armas 2006:6; Teruel 2006:50, 51, fig. 12 e; Teruel et al. 2006:220, 221, 223, fig. 1; Volschenk et al. 2008:653, 658, 659, 663, 664, 674, fig. 1D, tab. 1, tab. 2.

Material examined.—DOMINICAN REPUBLIC: *La Altagracia Province*: Parque Nacional del Este: Cabo Flaso (entrance zone), 18°22'25"N, 68°37'01"W, 14 July 2004, E.S. Volschenk & J. Huff, 67.7 m, 1 ♂ (AMNH [ESV6091]); Track between ranger station (at Boca de Yuma) and Punta Faustino, 18°21'17.2"N, 68°36'52.3"W, 14 July 2004, E.S. Volschenk & J. Huff, 3.3 m, dense canopy humid forest, hand collected at night with blacklights, from limestone outcrops, especially along an old rock wall along the start of the track, 1 ♀, 48 first instars (AMNH [ESV6010]), 1 ♀, 22 first instars (AMNH [ESV6019]), 1 ♀ 32 first instars (AMNH [ESV6039]), 11 ♂, 4 ♀, 1 subad. ♂, 1 subad. ♀, 2 juv. (AMNH [ESV6072]), 1

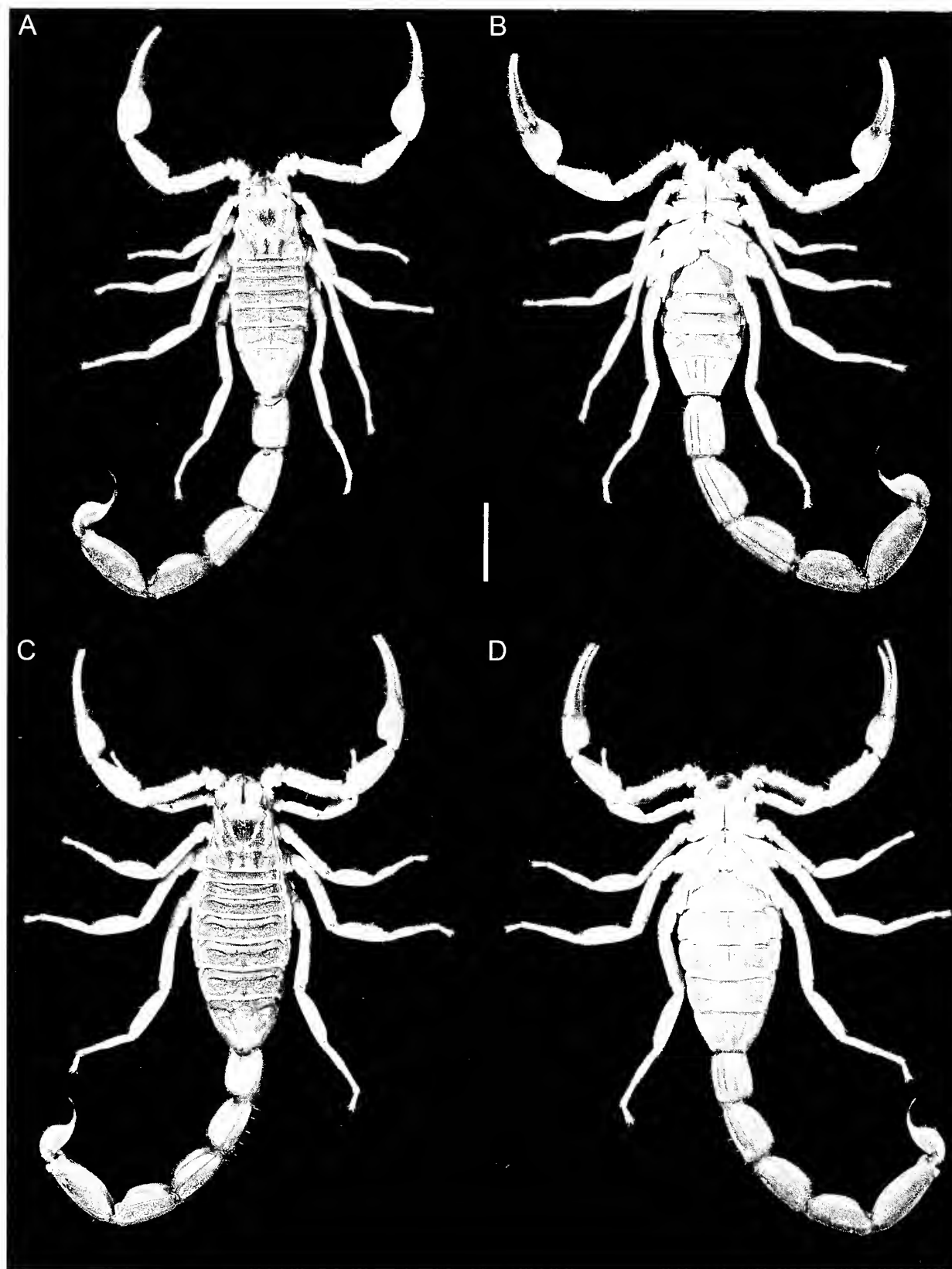


Figure 2.—*Rhopalurus abudi* Armas & Marcato Fondour 1987, habitus: A, B. ♂ (AMNH). C, D. ♀ (AMNH). A, C. Dorsal aspect. B, D. Ventral aspect. Scale bars = 5 mm.

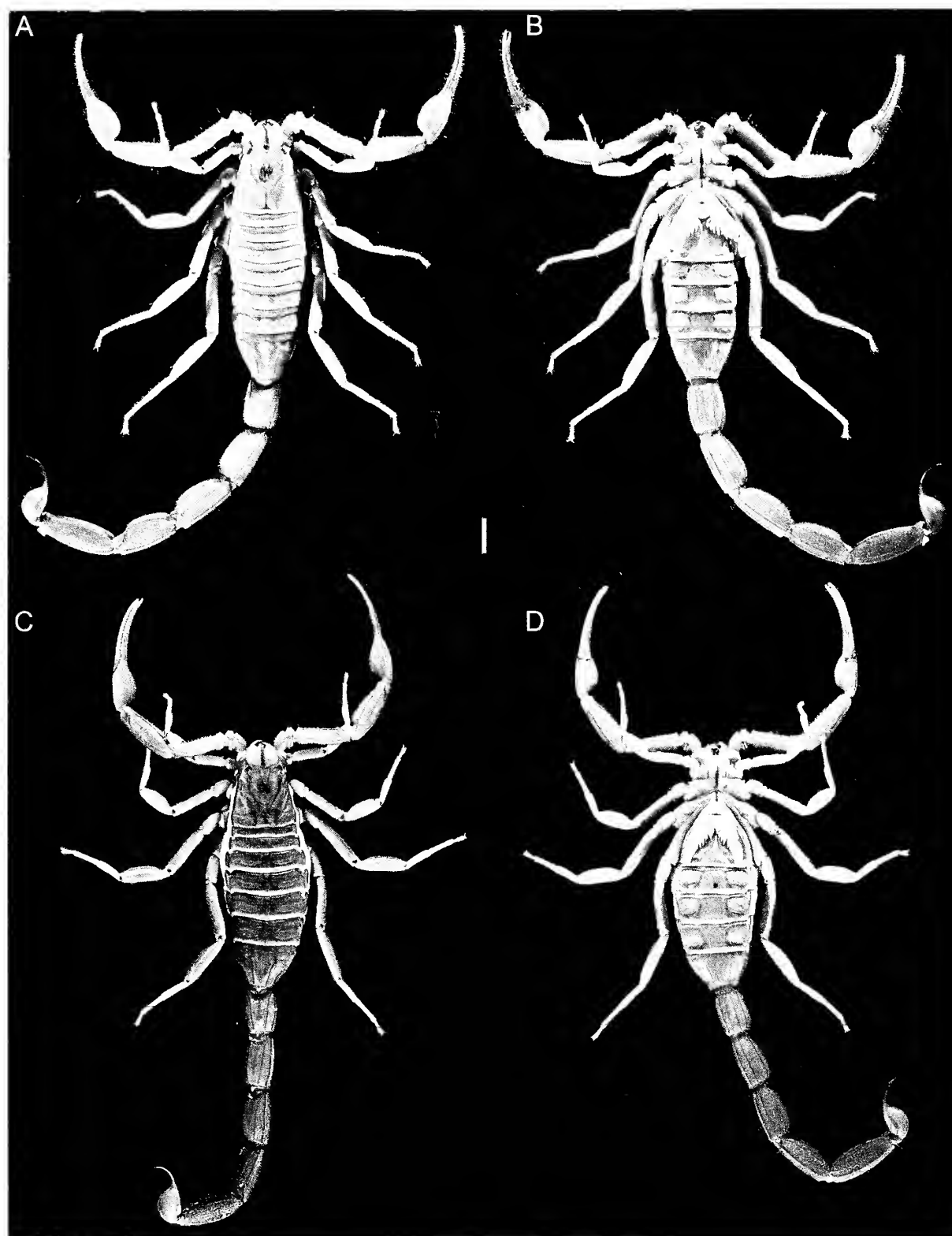


Figure 3.—*Rhopalurus bouettii* Armas 1999, habitus: A, B. ♂ (AMNH). C, D. ♀ (AMNH). A, C. Dorsal aspect. B, D. Ventral aspect. Scale bars = 5 mm.

♂, 1 ♀ (AMNH [ESV7110]), 1 ♂, 1 ♀ (AMNH [ESV7117]), 1 ♂, (AMNH [ESV7120]), 1 ♂, 1 ♀ (AMNH [ESV7242]), 1 ♂, 1 ♀ (AMNH [ESV7303]), 1 ♀ (AMNH [ESV7306]), 1 ♂, 1 ♀ (AMNH [ESV7705]), 1 ♂, 1 ♀ (AMNH [ESV7937]), 3 juv. (AMNH), 1 juv. (AMNH [LP 3268]).

Relationships.—Based on morphological similarity, *R. abudi* appears to be most closely related to *R. bouettii*, and was compared directly with the latter by Armas (1999: 127). When compared to *R. princeps*, the third *Rhopalurus* species occurring on Hispaniola, *R. abudi* and *R. bouettii* are similar

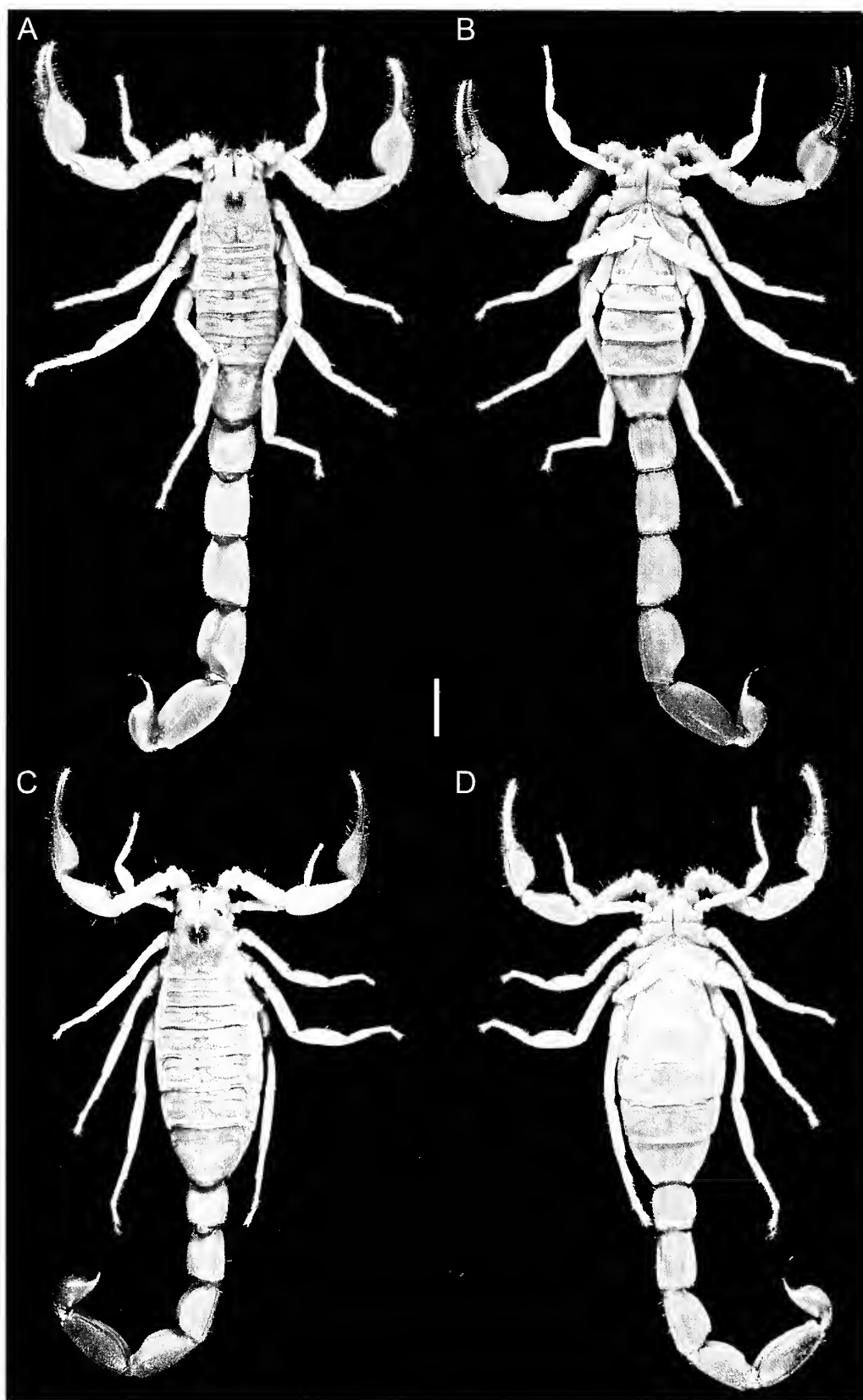


Figure 4.—*Rhopalurus princeps* (Karsch 1879), habitus: A, B. ♂ (AMNH). C, D. ♀ (AMNH). A, C. Dorsal aspect. B, D. Ventral aspect. Scale bars = 5 mm.

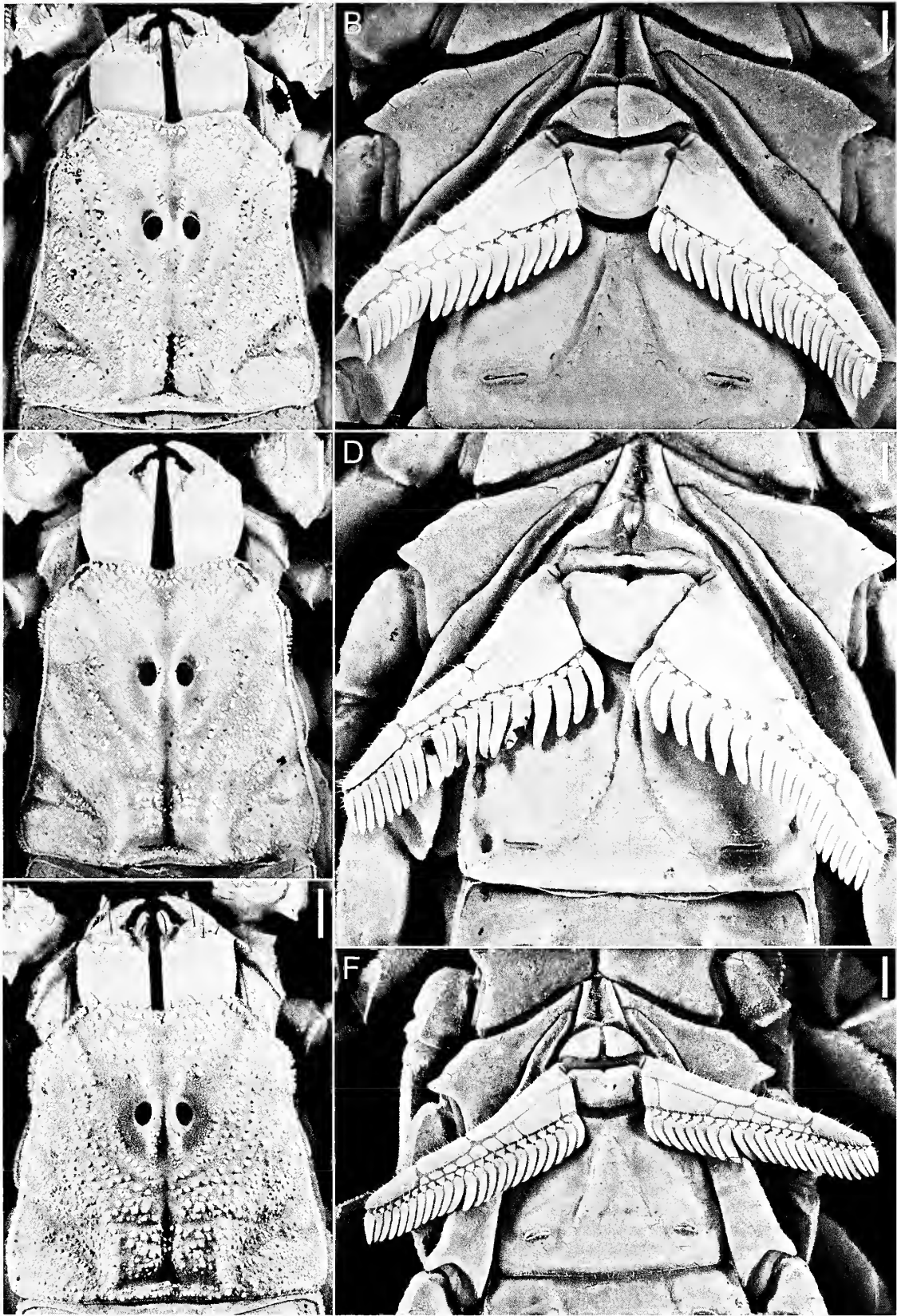


Figure 5.—Carapace, dorsal aspect (A, C, E), and sternum, genital operculum and pectines, ventral aspect (B, D, F): A, B. *Rhopalurus abudi* Armas & Marcato Fondour 1987, ♂ (AMNH). C, D. *Rhopalurus bouettii* Armas 1999, ♂ (AMNH). E, F. *Rhopalurus princeps* (Karsch 1879), ♂ (AMNH). Scale bars = 1 mm.

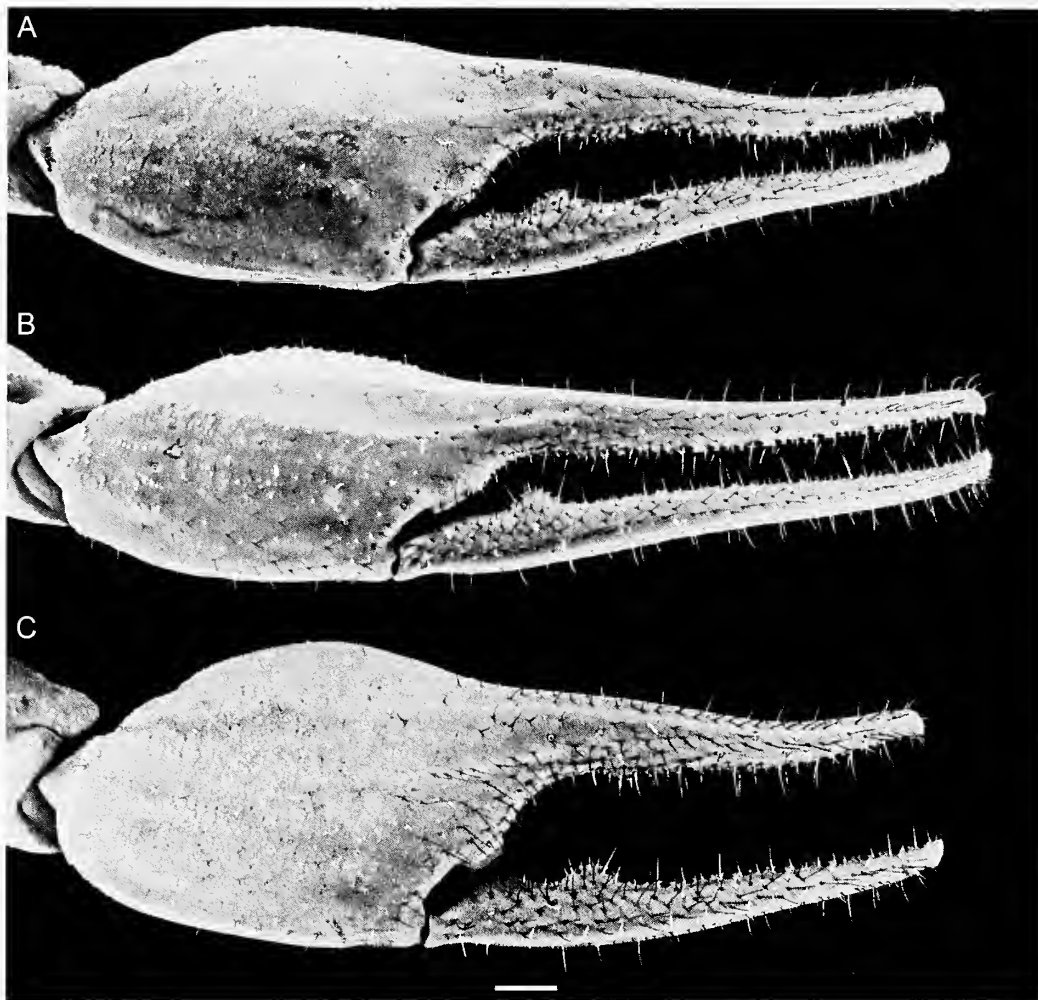


Figure 6.—Pedipalp chela manus, external aspect: A. *Rhopalurus abudi* Armas & Marciano Fondeur 1987, ♂ (AMNH). B. *Rhopalurus bonettii* Armas 1999, ♂ (AMNH). C. *Rhopalurus princeps* (Karsch 1879), ♂ (AMNH). Scale bar = 1 mm.

in carinal development and shape of the carapace (Figs. 5A, C, E; Tables 1–3); development of the pectines (Figs. 5B, D, F); carinal development and length of the pedipalp chela manus (Figs. 6, 7; Tables 1–3); and length of the metasomal segments (Figs. 8–11; Tables 1–3). Lourenço & Pinto-da-Rocha (1997:181) suggested that *R. abudi* may be a junior synonym of *R. princeps* but the two species differ in many respects (Figs. 2, 4, 5A, B, E, F, 6A, C, 7A, C). *Rhopalurus princeps* appears to be more closely related to *Rhopalurus* species on Cuba than to *R. abudi* and *R. bonettii*.

Diagnosis.—*Rhopalurus abudi* differs conspicuously from *R. bonettii* on the basis of the sexually dimorphic pedipalp chelae of the adult male. This dimorphism is well developed in *R. abudi*: the chela manus of the adult male is incrassate and the fingers strongly curved proximally (fixed finger curved dorsally, movable finger curved ventrally), such that only the distal portion of the fingers connect and a distinctive gap is present between them proximally, when closed (Fig. 6A). The chela manus of female *R. abudi* is not incrassate and the fingers are not curved proximally, such that the fingers connect along most of their length and little to no gap is present between them proximally, when closed (Fig. 7A). This dimorphism is considerably less developed in *R. bonettii*, in which the male and female chelae are similar, the manus of the

male being only slightly incrassate, relative to the female, and the fingers not curved proximally, such that the fingers connect along most of their length and little to no gap is present between them proximally, when closed (Figs. 6B, 7B).

The two species differ further in development of the pectines. The pectines of *R. bonettii* are very broad proximally, with a more pronounced basal plate (Armas 1999), and the first 6–7 pectinal teeth are noticeably larger than the rest (Fig. 5D), compared to *R. abudi*, in which the pectines are narrower proximally, with a less pronounced basal plate, and the pectinal teeth similar in size (Fig. 5B). These morphological differences appear to be associated with differences in behavior. In the field, *R. bonettii* was observed to stridulate more loudly than *R. abudi* (and *R. princeps*, in which the pectines are even less developed).

Other differences between the two species are as follows. The coloration of *R. abudi* is darker, due to extensive infuscation, than *R. bonettii*, which is pale (Armas 1999; Figs. 2, 3). The carapace, pedipalp chelae, legs and tergites are noticeably infuscated in *R. abudi* but pale in *R. bonettii*. The metasoma and telson of *R. abudi* are strongly infuscated laterally and ventrally, especially on segments II–IV, becoming more so distally, with each segment darker than the preceding one and segment V darkest. The metasoma and telson of *R.*

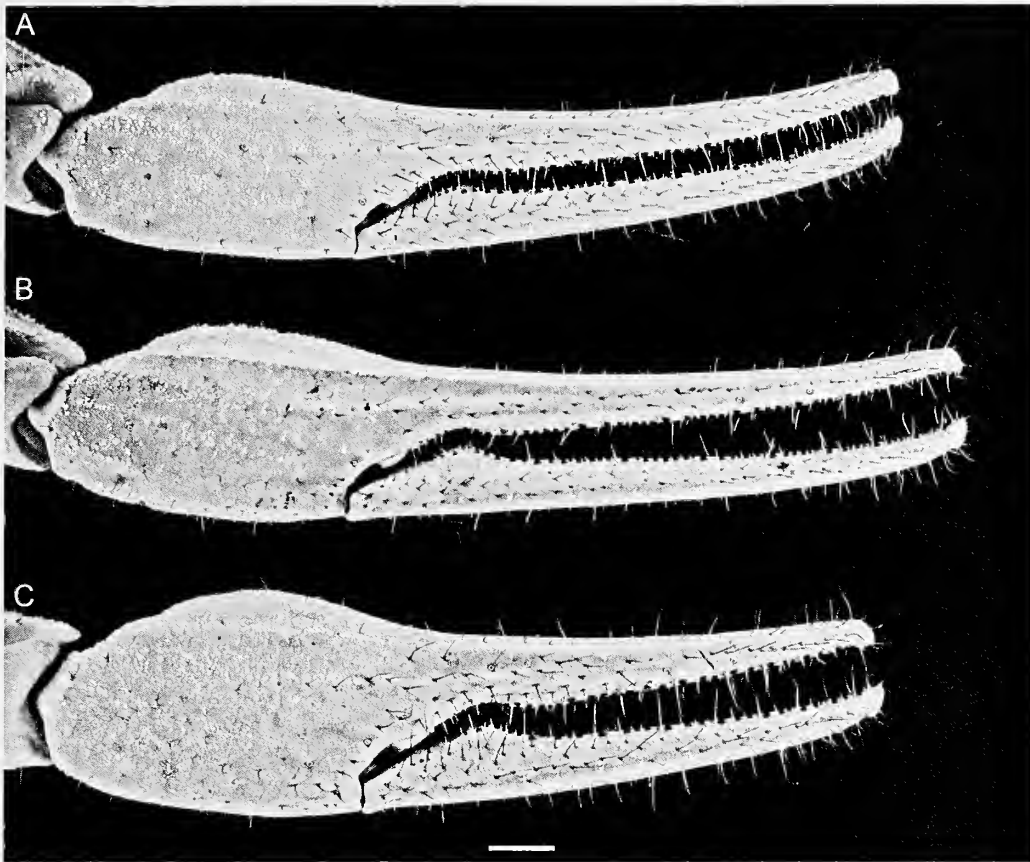


Figure 7.—Pedipalp chela manus, external aspect: A. *Rhopalurus abudi* Armas & Marciano Fondeur 1987, ♀ (AMNH). B. *Rhopalurus bonettii* Armas 1999, ♀ (AMNH). C. *Rhopalurus princeps* (Karsch 1879), ♀ (AMNH). Scale bar = 1 mm.

bonettii are weakly infuscated on segments III–V or IV and V only. The carapace and tergites are more coarsely and densely granular in *R. abudi* than in *R. bonettii*. The submedian sulci of sternite III are convergent in *R. abudi* and subparallel in *R. bonettii* (Armas & Marciano Fondeur 1987; Armas 1999; Figs. 15, 17). The pale, raised posteromedial surface of sternite V in the male is more prominent in *R. bonettii* than in *R. abudi*. The metasomal segments of *R. abudi* are shorter and broader (i.e., the width/length ratio is smaller) than those of *R. bonettii*, which are longer and narrower (i.e., the width/length ratio is greater) (Armas 1999; Figs. 8, 9, Tables 1, 2). The granulation, ventromedian, and ventrolateral carinae of metasomal segment V are less developed compared with those of the preceding segments such that the segment has a shinier, rounded appearance in *R. abudi* (Fig. 8). The granulation, ventromedian, and ventrolateral carinae of metasomal segment V are more developed in *R. bonettii* such that the segment has a matt, angular appearance (Fig. 9).

Description.—The following description is based on the specimens illustrated in Figs. 2, 5A, B, 6A, 7A, 8, 11 and listed in Table 1.

Coloration: Chelicerae brownish-yellow with finely reticulate infuscation on manus, becoming more intense distally; fingers brownish-yellow, not infuscated, teeth darker due to sclerotization. Carapace brownish-yellow with darker tan-brown patches of infuscation around median ocelli (Figs. 2A, C); lateral surfaces, carinae and lateral ocular tubercles with blackish-brown infuscation. Pedipalp femur and patella

brownish-yellow, carinae noticeably darker; femur lightly and uniformly infuscated; patella not infuscated; chela manus reddish-brown, darker than femur and patella, entirely infuscated, becoming gradually darker towards base of fingers; chela fingers infuscated, becoming gradually paler distally. Legs pale brownish-yellow; external surfaces of femur and patella lightly and uniformly infuscated. Mesosoma brownish-yellow with broad, transverse band across each tergite; pretergites infuscated, tan-brown; post-tergites with reticulate infuscation concentrated near carinae, becoming paler posteriorly; posterior margins pale brownish-yellow, not infuscated. Sternites tannish-brown, without infuscation; VII with darker carinae. Metasomal segments infuscated, becoming gradually darker ventrally and posteriorly, carinae darker than intercarinal surfaces; each segment darker than preceding segment, I and II, tan-brown, III, reddish-brown, IV and V, dark to very dark tan. Telson dark reddish-brown, not infuscated; aculeus black distally.

Chelicerae: Movable finger, ventral surface with two subdistal teeth; distal external and distal internal teeth equal, opposable. Fixed finger, ventral surface with single denticle; ventral surface with dense brush of long, fine macrosetae.

Carapace: Carapace coarsely and sparsely granular, mainly on interocular and lateral surfaces. Anterior and posterior margins of carapace procurved; anterior margin with shallow median notch (emargination), without median projection (epistome) (Fig. 5A). Lateral ocular tubercles each with three macro-ocelli and one (anterior) micro-ocellus, situated dorsal

Table 1.—Meristic data for three male and three female specimens of *Rhopalurus abudi* Armas & Marcato Fondeur 1987 deposited in the collection of the American Museum of Natural History (AMNH), New York. ¹ Sum of carapace, tergites I–VII, metasomal segments I–V, and telson; ² sum of tergites I–VII; ³ sum of metasomal segments I–V and telson; ⁴ measured along an axis parallel to the dorsal surface; ⁵ measured from base of condyle to tip of fixed finger.

Sex		♂	♂	♂	♀	♀	♀
Repository		AMNH	AMNH	AMNH	AMNH	AMNH	AMNH
Reference number		ESV7937	ESV7303	ESV7117	ESV7937	ESV7303	ESV7117
Total length ¹		67.45	69.71	68.75	77.48	91.67	87.83
Carapace	length	7.50	8.50	8.01	8.75	10.23	10.28
	anterior width	4.67	6.90	6.03	6.80	8.18	7.98
	posterior width	7.65	8.82	8.08	9.32	10.84	11.29
	eye diameter	0.63	0.74	0.63	0.72	0.79	0.73
	interocular distance	0.63	0.71	0.53	0.58	0.66	0.74
Mesosoma	total length ²	18.96	21.77	17.85	23.32	28.27	28.59
Sternite VII	length	5.08	5.93	4.89	5.86	7.08	6.92
	width	6.98	8.16	7.36	8.71	10.86	10.30
Metasoma	total length ³	48.42	54.51	53.08	54.16	63.36	63.36
Metasoma I	length	6.36	7.32	7.22	7.08	8.59	8.47
	width	4.37	5.03	4.69	5.00	5.73	5.82
	height	3.69	4.12	3.19	4.00	3.91	4.09
Metasoma II	length	7.48	8.30	8.13	8.29	9.70	9.91
	width	4.23	4.84	4.70	4.73	5.40	5.45
	height	3.52	4.01	3.73	4.06	4.69	4.63
Metasoma III	length	8.13	8.95	8.71	9.02	9.52	10.25
	width	4.18	5.03	4.81	4.59	5.41	5.48
	height	3.84	4.09	4.00	4.11	4.56	4.77
Metasoma IV	length	8.58	9.39	9.25	9.07	10.76	10.63
	width	4.39	5.03	4.89	4.72	5.29	5.46
	height	3.59	4.10	3.92	3.99	4.50	4.57
Metasoma V	length	9.99	11.32	10.88	11.27	13.33	12.87
	width	4.28	4.90	4.74	4.63	4.47	5.33
	height	3.54	4.12	3.79	4.01	4.53	4.79
Telson	total length ⁴	7.88	9.23	8.89	9.43	11.46	11.23
	vesicle length	4.44	5.26	5.15	5.22	6.43	6.38
	vesicle width	2.55	2.90	2.84	2.94	3.46	3.59
	vesicle height	2.55	2.91	2.67	2.90	3.44	3.49
	aculeus length	3.54	3.86	3.76	4.22	5.33	5.41
Pedipalp	total length ⁵	29.96	35.72	33.57	35.69	42.36	41.93
	trochanter length	3.74	4.24	3.49	3.92	4.47	4.72
Femur	length	6.92	7.49	7.32	8.02	9.05	8.74
	width	2.25	2.28	2.37	2.32	2.84	2.89
	height	1.43	1.83	1.71	1.81	2.54	2.05
Patella	length	7.45	8.92	8.66	8.99	10.98	10.57
	width	2.95	3.25	3.06	3.35	3.81	3.76
	height	2.06	2.35	2.24	2.55	2.85	2.84
Chela	length	11.85	15.07	14.10	14.76	17.86	17.90
	width	3.09	3.96	4.06	2.87	3.49	3.22
	height	3.39	4.03	4.00	2.97	3.53	3.49
	fixed finger length	6.73	8.26	7.56	8.99	10.75	10.74
	ventroexternal carina length	4.66	5.32	5.38	5.02	6.00	5.96
Pectines	movable finger length	8.67	10.06	9.23	10.01	12.16	12.22
	total length	7.57	7.79	7.12	7.36	8.74	8.43
	length along dentate margin	6.86	7.24	6.43	6.66	7.91	7.54
	tooth count (left/right)	23/23	23/23	22/23	20/20	22/21	20/20

to posterior macro-ocellus; posterior micro-ocellus absent. Median ocelli considerably larger than lateral ocelli, situated anteromedially. Median ocular macrosetae fine, acuminate; lateral ocular macrosetae absent. Ocular tubercle with pair of costate-granular superciliary carinae, protruding slightly above median ocelli. Five other pairs of costate-granular carinae present, disconnected. Anteromedian sulcus moderately deep, ovate; posteromedian sulcus narrow, shallow

anteriorly, deep posteriorly; posterolateral sulci shallow, wide, curved; posteromarginal sulcus deep, narrow.

Sternum: Subtriangular (Fig. 5B). Median longitudinal sulcus Y-shaped, shallow anteriorly, deep and narrow posteriorly.

Genital operculum: Completely divided longitudinally; macrosetae evenly distributed. Genital papillae present (♂), absent (♀).

Table 2.—Meristic data for three male and three female specimens of *Rhopalurus bonettii* Armas 1999 deposited in the collection of the American Museum of Natural History (AMNH), New York. ¹ Sum of carapace, tergites I–VII, metasomal segments I–V, and telson; ² sum of tergites I–VII; ³ sum of metasomal segments I–V and telson; ⁴ measured along an axis parallel to the dorsal surface; ⁵ measured from base of condyle to tip of fixed finger.

Sex		♂	♂	♂	♀	♀	♀
Repository		AMNH	AMNH	AMNH	AMNH	AMNH	AMNH
Reference number		ESV7112	ESV7127	ESV7126	ESV7127	ESV7112	ESV6005
Total length ¹		64.64	63.42	63.48	70.31	76.96	71.72
Carapace	length	7.33	7.22	7.35	7.63	9.30	7.89
	anterior width	5.55	5.38	5.33	5.91	7.09	6.10
	posterior width	7.16	6.99	7.51	7.67	9.51	7.58
	eye diameter	0.55	0.57	0.55	0.62	0.58	0.64
	interocular distance	0.52	0.56	0.50	0.61	0.53	0.55
Mesosoma	total length ²	18.10	18.35	18.93	21.24	23.48	21.44
Sternite VII	length	4.50	4.41	4.8	5.22	6.16	5.43
	width	6.53	6.09	6.53	7.48	8.76	7.56
Metasoma	total length ³	47.02	46.52	47.48	48.74	56.53	48.84
Metasoma I	length	6.31	6.28	6.14	6.54	7.66	6.84
	width	3.87	3.65	4.04	4.05	4.60	4.02
	height	3.35	3.28	3.59	3.52	4.02	3.46
Metasoma II	length	7.31	7.35	7.32	7.66	8.76	7.76
	width	3.89	3.60	3.80	4.02	4.43	3.67
	height	3.30	3.50	3.38	3.35	3.87	3.34
Metasoma III	length	7.84	7.90	8.05	7.85	9.18	8.04
	width	3.78	3.70	3.91	3.82	4.32	3.90
	height	3.36	3.38	3.42	3.50	3.96	3.32
Metasoma IV	length	8.18	7.79	8.29	8.52	9.86	7.79
	width	3.83	3.68	4.06	4.01	4.35	3.74
	height	3.36	3.29	3.44	3.69	3.77	3.41
Metasoma V	length	9.56	9.64	9.85	9.86	11.26	9.92
	width	3.77	3.63	4.03	3.62	4.25	3.68
	height	3.40	3.17	3.34	3.59	3.90	3.43
Telson	total length ⁴	7.82	7.56	7.83	8.31	9.81	8.49
	vesicle length	4.52	4.50	4.57	4.56	5.67	4.87
	vesicle width	2.59	2.46	2.73	2.75	3.27	2.88
	vesicle height	2.69	2.50	2.70	2.59	3.22	2.79
	aculeus length	3.22	3.77	3.16	3.98	4.99	3.74
Pedipalp	total length ⁵	32.64	31.82	33.49	34.96	40.85	35.35
	trochanter length	3.36	3.53	3.64	3.95	4.49	3.97
Femur	length	7.13	6.77	6.97	7.34	8.71	7.46
	width	2.10	1.98	2.08	2.20	2.71	2.26
	height	1.58	1.45	1.46	1.61	1.73	1.83
Patella	length	8.49	8.16	9.00	9.16	10.69	9.11
	width	2.79	2.63	3.05	2.91	3.28	3.01
	height	2.06	2.02	2.08	2.24	2.53	2.13
Chela	length	13.66	13.36	13.88	14.51	16.96	14.81
	width	2.84	2.85	3.20	2.76	3.07	2.77
	height	2.98	2.94	3.28	2.76	3.21	3.10
	fixed finger length	7.55	6.87	7.54	8.63	10.21	8.33
	ventroexternal carina length	4.44	4.65	4.76	4.88	5.71	4.72
Pectines	movable finger length	9.02	9.04	9.32	9.93	11.59	9.96
	total length	7.05	6.35	6.53	6.89	7.50	6.47
	length along dentate margin	6.43	6.00	6.22	5.93	6.82	5.93
	tooth count (left/right)	24/23	22/23	22/21	21/20	20/20	19/19

Pectines: Pectines broad (Fig. 5B), dorsal surfaces with stridulatory nodules. First proximal median lamella unmodified in ♀. Fulcrum prominent. Proximal pectinal teeth not noticeably larger than others in ♂ and ♀. Pectinal tooth counts, 17–24 (♂), 19–22 (♀).

Pedipalps: Femur with five distinct carinae; dorsoexternal, dorsointernal, ventrointernal and externomedian carinae continuous, costate-granular; internomedian carina discontin-

uous, comprising row of isolated spiniform granules; externo-median and dorsoexternal carinae each with an acuminate macroseta distally; intercarinal surfaces finely and uniformly granular.

Patella with seven distinct carinae; dorsomedian, dorsoin-ternal, ventrointernal, ventroexternal, externomedian, dor-soexternal carina continuous, costate-granular; internomedian carina discontinuous, comprising several large, well-spaced

Table 3.—Meristic data for three male and three female specimens of *Rhopalurus princeps* (Karsch 1879) deposited in the collection of the American Museum of Natural History (AMNH), New York. ¹ Sum of carapace, tergites I–VII, metasomal segments I–V, and telson; ² sum of tergites I–VII; ³ sum of metasomal segments I–V and telson; ⁴ measured along an axis parallel to the dorsal surface; ⁵ measured from base of condyle to tip of fixed finger.

Sex		♂	♂	♂	♀	♀	♀
Repository		AMNH	AMNH	AMNH	AMNH	AMNH	AMNH
Locality or number		Is. Cabritos	ESV6033	LP 3260	Is. Cabritos	ESV6033	LP 3260
Total length ¹		59.90	47.27	51.19	69.19	66.32	55.21
Carapace	length	6.62	5.63	6.38	7.90	7.18	7.03
	anterior width	5.33	4.65	5.12	6.59	5.81	5.59
	posterior width	6.97	5.84	6.95	8.44	7.45	7.24
	eye diameter	0.58	0.46	0.45	0.62	0.52	0.48
	interocular distance	0.40	0.43	0.47	0.46	0.63	0.48
Mesosoma	total length ²	17.67	14.00	17.06	21.87	20.58	19.23
Sternite VII	length	4.65	3.59	4.36	5.53	5.02	4.31
	width	6.43	5.51	6.60	8.36	7.81	7.68
Metasoma	total length ³	42.90	35.94	41.52	49.00	45.32	45.63
Metasoma I	length	5.50	4.76	5.08	6.30	5.91	5.26
	width	4.19	3.24	4.11	4.90	4.30	4.50
	height	3.39	2.98	3.54	3.85	3.69	3.61
Metasoma II	length	6.55	5.47	6.17	7.24	6.72	6.85
	width	4.11	3.26	4.13	4.59	4.14	4.39
	height	3.39	2.86	3.43	3.89	3.68	3.62
Metasoma III	length	7.16	5.86	6.73	7.56	7.24	7.55
	width	4.16	3.53	4.24	4.74	4.22	4.30
	height	3.52	2.96	3.49	3.97	3.70	3.72
Metasoma IV	length	7.45	6.05	7.28	7.87	7.39	8.08
	width	4.65	3.67	4.51	4.93	4.52	4.55
	height	3.58	3.02	3.61	3.96	3.69	3.69
Metasoma V	length	9.03	7.46	8.91	11.37	9.51	9.62
	width	4.67	3.54	4.50	4.86	4.30	4.35
	height	3.40	2.89	3.42	3.81	3.63	3.60
Telson	total length ⁴	7.21	6.34	7.35	8.66	8.55	8.27
	vesicle length	4.70	3.93	4.69	5.41	5.45	4.85
	vesicle width	2.51	2.41	2.62	3.27	3.06	2.99
	vesicle height	2.51	2.29	2.52	3.02	2.94	2.87
	aculeus length	3.40	2.48	3.46	3.77	4.05	4.61
Pedipalp	total length ⁵	28.26	23.46	26.93	32.75	29.12	28.23
	trochanter length	3.21	2.71	2.87	4.20	3.40	3.44
Femur	length	6.14	4.73	5.54	7.12	6.28	5.86
	width	1.97	1.68	1.80	2.36	2.05	1.74
	height	1.72	1.40	1.61	1.96	1.82	1.74
Patella	length	6.98	6.17	6.94	7.97	7.45	7.18
	width	2.75	2.24	1.98	3.23	2.91	2.91
	height	2.10	1.84	2.44	2.56	2.22	2.25
Chela	length	11.93	9.85	11.58	13.46	11.99	11.75
	width	3.51	2.83	3.52	3.33	2.95	2.98
	height	3.54	2.81	3.39	3.40	3.02	2.89
	fixed finger length	5.45	4.34	5.06	6.58	6.00	6.08
	ventroexternal carina length	4.95	4.15	4.78	4.85	4.76	4.40
Pectines	movable finger length	7.07	6.05	6.94	8.25	7.98	7.28
	total length	6.34	5.14	6.67	6.99	6.25	5.75
	length along dentate margin	6.10	5.03	6.18	6.50	5.37	5.22
	tooth count (left/right)	25/24	24/25	25/26	22/23	21/22	21/20

spiniform granules proximally, becoming smaller distally; proximal tubercle moderately developed; dorsointernal carina not fused with ventrointernal carina; intercarinal surfaces smooth, except for ventral surface which is finely granular.

Chela manus (♂) incrassate, length along ventroexternal carina 33–51% greater than manus width, 32–37% greater than manus height (Table 1), fingers strongly curved proximally (fixed finger curved dorsally, movable finger curved

ventrally), such that only connect distally and distinctive gap present between them proximally, when closed (Fig. 6A); manus (♀) not incrassate, length along ventroexternal carina 72–85% greater than manus width, 69–71% greater than manus height (Table 1), fingers not curved proximally, such that connect along most of length and little to no gap present between them proximally when closed (Fig. 7A). Chela with five distinct carinae; dorsomedian, dorsal secondary and

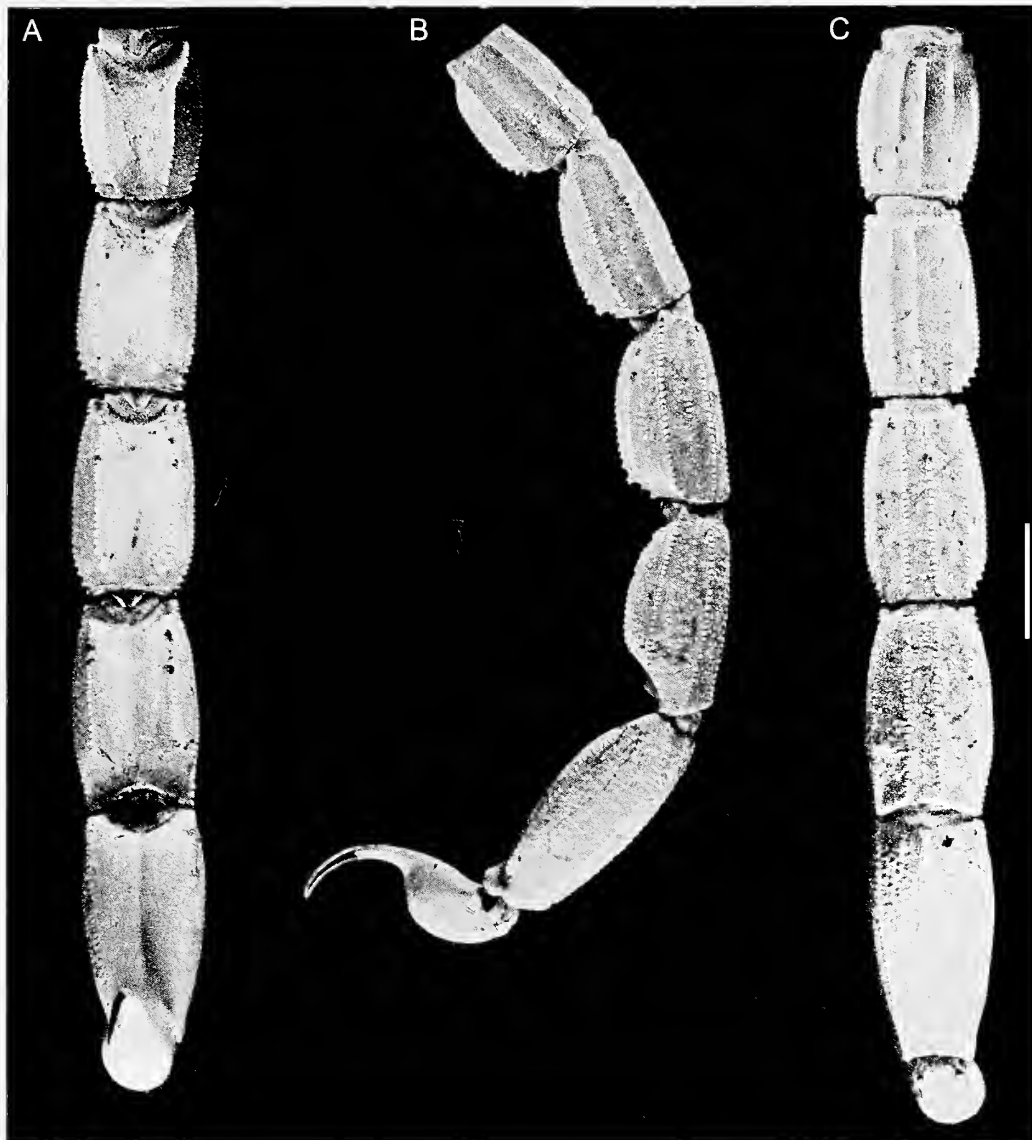


Figure 8.—*Rhopalurus abudi* Armas & Marciano Fondeur 1987, ♂ (AMNH), metasomal segments I–V and telson: A. Dorsal aspect. B. Lateral aspect. C. Ventral aspect. Scale bar = 1 mm.

ventroexternal carinae continuous, costate-granular (Figs. 6A, 7A); digital carina continuous, costate-granular, becoming obsolete proximally; dorsointernal carina discontinuous, comprising row of small granules distally, becoming obsolete proximally; other carinae absent; intercarinal surfaces smooth, except for internal surface where several low granules present. Movable finger with small lobe (eminence) proximally; movable finger length 72–89% (♂) or 99–105% (♀) greater than length along ventroexternal carina (Table 1); dentate margins of fixed and movable fingers each with eight oblique denticle rows, in addition to short apical row of four denticles; each row terminating in large denticle at proximal and distal ends; rows slightly imbricated, terminal denticle of each row displaced distally from the main row by space of one or more denticles; internal and external supernumerary denticles present in addition to internal and external accessory denticles; fingers each with an enlarged terminal denticle.

Trichobothria: Orthobothriotaxic, Type A, α configuration (femoral trichobothria d_1 and d_4 situated closer to dorsoex-

ternal carina than d_3), with the following segment totals: femur 11 (5 dorsal, 4 internal, 2 external), patella 13 (5 dorsal, 1 internal, 7 external), and chela 15 (8 manus, 7 fixed finger). Total number of trichobothria per pedipalp, 39. Femoral trichobothrium d_2 similar in size to d_1 , situated internal to dorsointernal carina; d_4 smaller than d_1 ; d_5 situated distinctly proximal to e_1 ; e_1 considerably smaller than e_2 . Patellar trichobothrium d_2 considerably smaller than d_1 ; d_3 situated external to dorsomedian carina. Chela trichobothrium Eb_1 smaller than Eb_2 and Eb_3 ; Eb_1 – Eb_3 situated proximally on manus; V_2 larger than, and situated close to V_1 ; Est smaller than Em and Et , which are similar in size; esb smaller than eb ; esb and eb situated near base of fixed finger; db situated between est and et ; dt situated distal to et .

Legs: I and II, tibiae and basitarsi each with paired rows of fine, acuminate macrosetae on pro- and retrolateral surfaces. III and IV, tibiae without spurs; basitarsi prolateral pedal spur with one acuminate seta, basal lobe pointed and stout; retrolateral pedal spur asetose. I–IV, telotarsi each with paired



Figure 9.—*Rhopalurus bonettii* Armas 1999, ♂ (AMNH), metasomal segments I–V and telson: A. Dorsal aspect. B. Lateral aspect. C. Ventral aspect. Scale bar = 1 mm.

ventrosubmedian rows of fine, acuminate macrosetae; laterodistal lobes truncated; median dorsal lobes extending to ungues; ungues short, distinctly curved, equal in length.

Mesosoma: Tergites entirely granular, finely on pretergites, coarsely on post-tergites, becoming more so distally; I–VII each with a strongly developed, granular dorsomedian carina; VII additionally with distinct pairs of costate-granular dorsosubmedian and dorsolateral carinae. Sternites III–VI smooth, acarinate, each with pair of narrow, slit-like respiratory spiracles (Figs. 2B, D); III with smooth, raised ridge medially, with stridulatory granules submedially; V with prominent pale, raised surface posteromedially in adult ♂, and 6–10 evenly spaced short, acuminate macrosetae along posterior margin; VII finely granular laterally and medially,

with pair of costate-granular ventrosubmedian and ventrolateral carinae.

Metasoma: Segments I–V progressively increasing in length (Fig. 8; Table 1), segment V 51–57% (♂) or 52–59% (♀) longer than segment I; segments stout, width/length segment I, 65–69% (♂) or 69–71% (♀), II, 57–58% (♂) or 55–57% (♀), III, 51–56% (♂) or 51–57% (♀), IV, 51–54% (♂) or 49–52% (♀), and V, 43–44% (♂) or 34–41% (♀). Intercarinal surfaces uniformly finely granular. Segments I–IV, paired dorsosubmedian and dorsolateral carinae continuous, costate-granular, granules gradually becoming larger posteriorly, without associated macrosetae; paired ventrolateral and ventrosubmedian carinae continuous, costate-granular, granules subequal; median lateral carinae continuous, costate-granular, fully developed

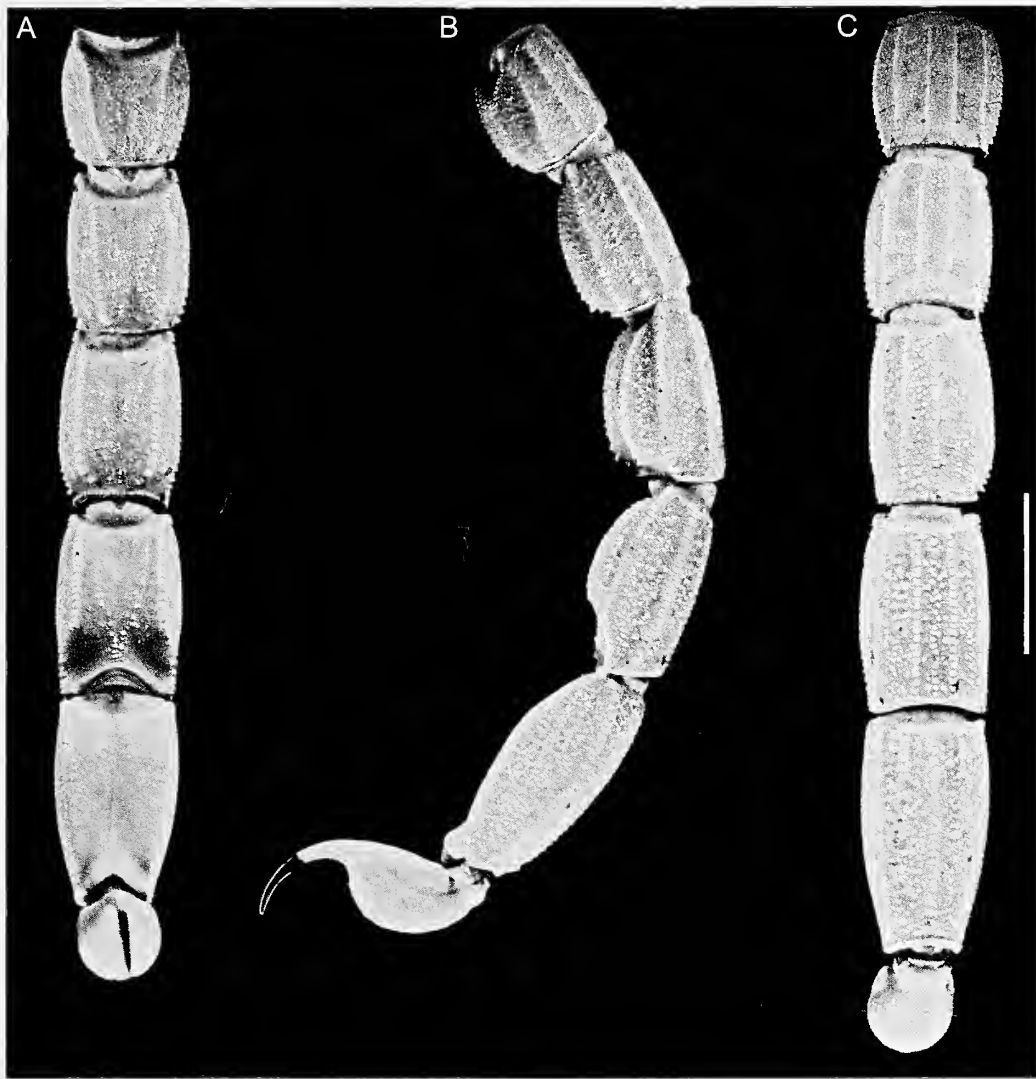


Figure 10.—*Rhopalurus princeps* (Karsch 1879), ♂ (AMNH), metasomal segments I–V and telson: A. Dorsal aspect. B. Lateral aspect. C. Ventral aspect. Scale bar = 1 mm.

on segment I, obsolete, granular, restricted to the posterior two-thirds of segment II, absent on segments III–V. Segment V, dorsosubmedian carinae absent; dorsolateral and ventrolateral carinae continuous, costate-granular, granules subequal; ventrosubmedian carinae obsolete, granular, reduced to anterior half of segment; ventromedian carina continuous, costate-granular, granules subequal, without posterior bifurcation.

Telson: Vesicle globose, height/length 52–57%, with flat dorsal surface and rounded ventral surface, slightly compressed anteroventrally (Table 1); slightly narrower than metasomal segment V, width 59–60% (♂) or 63–77% (♀) of segment V. Subaculear tubercle absent (Fig. 8B). Ventrolateral and ventrosubmedian carinae absent; ventromedian carina continuous, granular. Vesicle surfaces with scattered granules, sparse microsetae, and fewer than 16 macrosetae. Aculeus long, 73–80% (♂) to 81–85% (♀) of vesicle length (Table 1), strongly curved.

Male hemispermatophore: Flagelliform, flagellum gradually tapering along its length, folded against shaft (Fig. 11); basal process lobate longitudinally; distal process terminating

adjacent to base of flagellum (in dorsal aspect), rib-like and extending longitudinally; distal lobe represented by shelf at base of flagellum; median lobe not developed; internobasal inflection absent; external lobe present, separated from distal process; with small, longitudinally-oriented costate process.

Female reproductive system: Ovariuterine network comprising three longitudinal and ten transverse tubules, forming eight “cells.”

Geographic variation: The single male specimen from Cabo Flaso is similar to those from the track between Boca de Yuma and Punta Faustino.

Ontogenetic variation: As in other species of *Rhopalurus*, male closely resembles female until the final instar; however, juveniles and subadults may be sexed by examination of the pectines and genital aperture.

Sexual dimorphism: In addition to aforementioned characters, adult males are proportionally longer than adult females. The increased length of the male is attributed mainly to the longer metasomal segments, which sum to 72–78% of the total length of males, but to 69–72% of the total length of females. Adult males are slightly more slender than adult females:

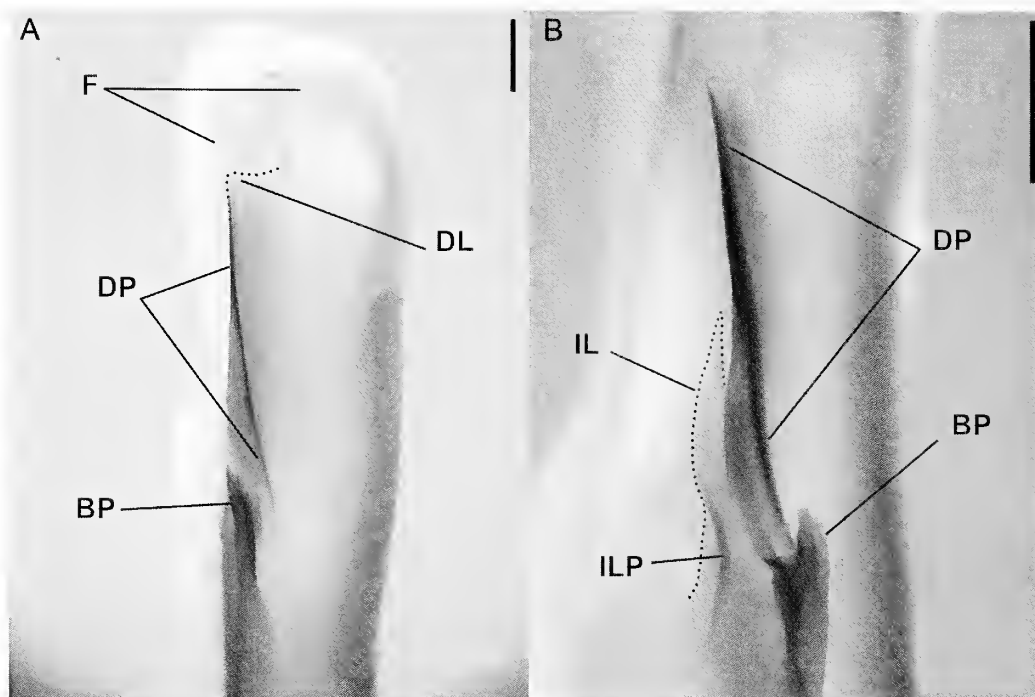


Figure 11.—*Rhopalurus abudi* Armas & Marcano Fondeur 1987, ♂ (AMNH), left hemispermatophore: A. External aspect. B. Anterior aspect (left view rotated right 90° around longitudinal axis). Abbreviations: F, flagellum; DL, distal lobe; DP, distal process; BP, basal process; IL, internal lobe; ILP, internal lobe process. Scale bars = 0.5 mm.

sternite VII length is 37–51% greater than its width in males and 49–53% greater in females (Table 1). The coloration of adult females is similar to but darker than that of adult males.

Distribution.—*Rhopalurus abudi* was described from Catuano, Isla Saona, off the southeast coast of the DR (Armas & Marcano Fondeur 1987). No new records of this species have been reported in the literature since the original description (Armas & Marcano Fondeur 1987; Armas et al. 1999; Teruel 2005, 2006). The records reported here, therefore, represent the first for this species on mainland Hispaniola. Based on published records and those obtained during our expedition, *R. abudi* appears to be restricted to humid coastal forest in the southeast of mainland DR and Isla Saona (Fig. 1). *Rhopalurus princeps* inhabits dry scrub in the central part of Hispaniola, including the valley of the Yaque del Norte River, the Neiba Valley, the Sierra de Baoruco, Sierra de Martín García, and Sierra de Ocoa (Teruel 2006). *Rhopalurus bonettii* is restricted to dry spiny forests south of the Sierra de Baoruco in the western part of mainland DR and Isla Beata, the type locality. The plotted locality data agree with Teruel's (2006: 51, fig. 12) map illustrating the approximate distributions of the three species.

Ecology.—*Rhopalurus abudi* is probably restricted to humid forests, a habitat not previously reported for any *Rhopalurus* species. Although collections were made on the western and eastern sides of Parque Nacional del Este during the course of our expedition, no specimens were found on the western side, which is drier and dominated by dense, spiny forest. Whereas the South American species of *Rhopalurus* appear to be restricted to savannas (Lourenço 1996, 2008), those of the Caribbean are also found in other vegetation zones, including forest (Armas 2001). During our expedition, *R. abudi* was

collected in lowland coastal humid forest on limestone, *R. bonettii* in dry spiny forests on limestone, and *R. princeps* in dry scrub on mixed substrata. All specimens of *R. abudi* were collected at night using UV light detection. None were found during the day, unlike *R. bonettii*, which was commonly found sheltering between slabs of rock (though never under bark or wood), and *R. princeps*, which was found under bark, wood and stones, as well as in dead and dry agave plants. The holotype of *R. abudi* was collected from under a stone (Armas & Marcano Fondeur 1987).

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LITERATURE CITED

- Armas, L.F. de. 1999. Quince nuevos alacranes de La Española y Navassa, Antillas Mayores (Arachnida: Scorpiones). *Avicennia* 10/11:109–144.
- Armas, L.F. de. 2001. Scorpions of the Greater Antilles, with the description of a new troglitic species (Scorpiones: Diplocentridae). Pp. 245–253. *In* Scorpions 2001. *In Memoriam* Gary A. Polis. (V. Fet & P.A. Selden, eds.). British Arachnological Society, Burnham Beeches, Buckinghamshire, UK.
- Armas, L.F. de. & E. de J. Marcano Fondev. 1987. Nuevos escorpiones (Arachnida: Scorpiones) de República Dominicana. *Poeyana* 356:1–24.
- Armas, L.F. de., J.A. Ottenwalder & K.A. Guerrero. 1999. Escorpiones de las Islas Saona, Beata y Catalina, República Dominicana (Arachnida: Scorpiones). *Cocuyo* 8:30–32.
- Borelli, A. 1910. Scorpioni nuovi o poco noti del Brasile. *Bollettino dei Musei di Zoologia ed Anatomia Comparata della Reale Università di Torino* 25(629):1–8.
- Fet, V., B. Gantenbein, A.V. Gromov, G. Lowe & W.R. Lourenço. 2003. The first molecular phylogeny of Buthidae (Scorpiones). *Euscorpius* 4:1–10.
- Fet, V. & G. Lowe. 2000. Family Buthidae C.L. Koch, 1837. Pp. 54–286. *In* Catalog of the Scorpions of the World (1758–1998). (V. Fet, W.D. Sissom, G. Lowe & M.E. Braunwalder, eds.). New York Entomological Society, New York.
- Flórez, E. 2001. Escorpiones de la familia Buthidae (Chelicerata: Scorpiones) de Colombia. *Biota Colombiana* 2(1):25–30.
- Francke, O.F. 1977. Two emendations to Stahnke's (1974) Vaejovidae revision (Scorpionida, Vaejovidae). *Journal of Arachnology* 4:125–135.
- González-Sponga, M.A. 1996. Guía para identificar escorpiones de Venezuela. Cuadernos Lagoven, Caracas. 204 pp.
- Hjelle, J.T. 1990. Anatomy and Morphology. Pp. 9–63. *In* The Biology of Scorpions. (G.A. Polis, ed.). Stanford University Press, Stanford, California.
- Kovářík, F. 1998. Štíři [Scorpions]. Madagaskar, Jihlava. 175 pp. [in Czech]
- Lamoral, B.H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). *Annals of the Natal Museum* 23:497–784.
- Lenarducci, Á.R.I.P., S.M. Lucas & R. Pinto-da-Rocha. 2005. Descrição de uma nova espécie de *Rhopalurus* Thorell, 1876 (Scorpiones: Buthidae) do nordeste brasileiro. *Biota Neotropica* 5(1a):1–8.
- Lourenço, W.R. 1979. A propos de la véritable identité des genres *Rhopalurus* Thorell, 1876 et *Centruroides* Marx, 1889 (Scorpiones, Buthidae). *Revue Arachnologique* 2:213–219.
- Lourenço, W.R. 1982. Révision du genre *Rhopalurus* Thorell, 1876 (Scorpiones, Buthidae). *Revue Arachnologique* 4:107–141.
- Lourenço, W.R. 1984. Complementary notes on the systematics of the genus *Rhopalurus* for the Caribbean area (Scorpiones, Buthidae). *Revista Brasileira da Biologia* 44:169–170.
- Lourenço, W.R. 1986. Biogéographie et phylogénie des scorpions du genre *Rhopalurus* Thorell, 1876 (Scorpiones, Buthidae). *Mémoires de la Société Royale Belge d'Entomologie* 33:129–137.
- Lourenço, W.R. 1996. The biogeography of scorpions. *Revue Suisse de Zoologie* 103:437–448.
- Lourenço, W.R. 2002. Nouvelles additions à la faune de scorpions néotropicaux (Arachnida). *Revue Suisse de Zoologie* 109:127–141.
- Lourenço, W.R. 2007. New considerations on the taxonomic status of the genus *Physoctonus* Mello-Leitão, 1934 (Scorpiones, Buthidae). *Boletín de la Sociedad Entomológica Aragonesa* 40:359–365.
- Lourenço, W.R. 2008. The geographic pattern of distribution of the genus *Rhopalurus* Thorell, 1876 in the Guayana-Amazon region (Scorpiones: Buthidae). *Euscorpius* 73:1–14.
- Lourenço, W.R., R.L.C. Baptista & A.P. de L. Giupponi. 2004. Troglitic scorpions: a new genus and species from Brazil. *Comptes Rendus Biologie* 327:1151–1156.
- Lourenço, W.R. & J.L. Cloudsley-Thompson. 1995. Stridulatory apparatus and the evolutionary significance of sound production in *Rhopalurus* species (Scorpiones: Buthidae). *Journal of Arid Environments* 31:423–429.
- Lourenço, W.R. & R. Pinto-da-Rocha. 1997. A reappraisal of the geographic distribution of the genus *Rhopalurus* Thorell (Scorpiones, Buthidae) and description of two new species. *Biogeographica* 73:181–191.
- Pocock, R.I. 1904. On a new stridulating-organ in scorpions discovered by W.J. Burchell in Brazil in 1828. *Annals and Magazine of Natural History (Series 7)* 13:56–62.
- Prendini, L. 2001a. Substratum specialization and speciation in southern African scorpions: The Effect Hypothesis revisited. Pp. 113–138. *In* Scorpions 2001. *In Memoriam* Gary A. Polis. (V. Fet & P.A. Selden, eds.). British Arachnological Society, Burnham Beeches, Buckinghamshire, UK.
- Prendini, L. 2001b. Further additions to the scorpion fauna of Trinidad and Tobago. *Journal of Arachnology* 29:173–188.
- Prendini, L., E.S. Volschenk, S. Maaliki & A.V. Gromov. 2006. A 'living fossil' from Central Asia: The morphology of *Pseudochactas ovchinnikovi* Gromov, 1998 (Scorpiones: Pseudochactidae), with comments on its phylogenetic position. *Zoologischer Anzeiger* 245:211–248.
- Rudloff, J.-P. 1994. Die Skorpionsfauna der Antillen (Arachnida: Scorpiones). Teil I. *Arthropoda* 2:3–12.
- Sissom, W.D. 1990. Systematics, biogeography, and paleontology. Pp. 64–160. *In* The Biology of Scorpions. (G.A. Polis, ed.). Stanford University Press, Stanford, California.
- Stahnke, H.L. 1970. Scorpion nomenclature and mensuration. *Entomological News* 81:297–316.
- Teruel, R. 2005. Nuevos datos sobre la taxonomía, distribución geográfica y ecología de los escorpiones de la República Dominicana (Scorpiones: Liochelidae, Scorpionidae, Buthidae). *Boletín de la Sociedad Entomológica Aragonesa* 36:165–176.
- Teruel, R. 2006. Apuntes sobre la taxonomía y biogeografía del género *Rhopalurus* Thorell 1876 (Scorpiones: Buthidae), con la descripción de dos nuevas especies de Cuba. *Boletín de la Sociedad Entomológica Aragonesa* 38:43–54.
- Teruel, R. & L.F. de Armas. 2006. Un nuevo *Rhopalurus* Thorell 1876 (Scorpiones: Buthidae) de Cuba oriental. *Boletín de la Sociedad Entomológica Aragonesa* 39:175–179.
- Teruel, R., V. Fet & M.R. Graham. 2006. The first mitochondrial DNA phylogeny of Cuban Buthidae (Scorpiones: Buthoidea). *Boletín de la Sociedad Entomológica Aragonesa* 39:219–226.

- Teruel, R. & C.A. Roncallo. 2008. Rare or poorly known scorpions from Colombia. III. On the taxonomy and distribution of *Rhopalurus laticauda* Thorell, 1876 (Scorpiones: Buthidae), with description of a new species of the genus. *Euscorpius* 68:1–12.
- Teruel, R. & A.K. Tietz. 2008. The true identity of *Rhopalurus pinto* Mello-Leitão, 1932, with notes on the status and distribution of *Rhopalurus crassicauda* Caporiacco, 1947 (Scorpiones: Buthidae). *Euscorpius* 70:1–14.
- Vachon, M. 1973 [1974]. Étude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les scorpions. *Bulletin du Muséum National d'Histoire Naturelle*, Paris (3) 140:857–958.
- Volschenk, E.S. 2005. A new technique for examining surface morphosculture of scorpions. *Journal of Arachnology* 33: 820–825.
- Volschenk, E.S., C.I. Mattoni & L. Prendini. 2008. Comparative anatomy of the mesosomal organs of scorpions (Chelicerata, Scorpiones), with implications for the phylogeny of the order. *Zoological Journal of the Linnean Society* 154:651–675.

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Appendix 1. Currently recognized species and subspecies of *Rhopalurus* Thorell 1876 and related genera, with countries, departments (Colombia, Haiti), provinces (Cuba, Dominican Republic), regions (French Guiana) and states (Brazil, Venezuela) of known distribution (data from González-Sponga 1996; Fet & Lowe 2000; Flórez 2001; Teruel 2006; Teruel & Roncallo 2008; Teruel & Tietz 2008; Lourenço 2008; this study). New records reported in this study are marked with an asterisk.

Physoctonus debilis (C.L. Koch 1840): Brazil (Bahia, Ceará, Pernambuco*, Piauí). This species was originally placed in the non-buthid genus *Vaejovis* C.L. Koch 1836. It was transferred to *Rhopalurus* by Borelli (1910) and remained there until Lourenço (2002) resurrected the genus *Physoctonus* Mello-Leitão 1934, earlier synonymized with *Rhopalurus* by Francke (1977).

Rhopalurus abudi Armas & Marciano Fondeur 1987: Dominican Republic (La Altagracia, La Romana).

Rhopalurus acromelas Lutz & Mello 1922: Brazil (Bahia, Ceará, Tocantins, Maranhão*, Pernambuco, Piauí).

Rhopalurus agamemnon (C.L. Koch 1839): Brazil (Bahia, Ceará, Tocantins, Mato Grosso, Pernambuco, Piauí).

Rhopalurus anazonicus Lourenço 1986: Brazil (Pará).

Rhopalurus bonettii Armas 1999: Dominican Republic (Pedernales).

Rhopalurus caribensis Teruel & Roncallo 2008: Colombia (Atlántico, La Guajira, Magdalena), Venezuela (Zulia). Lourenço (2008) suggested that this species might be more appropriately recognized as a subspecies of *Rhopalurus laticauda* Thorell 1876.

Rhopalurus crassicauda Caporiacco 1947: Brazil (Amazonas*, Roraima), Guyana. This species was synonymized with *Rhopalurus pinto* Mello-Leitão 1933 by Lourenço (1982) and reinstated by Lourenço (2002). Teruel & Tietz (2008) demonstrated that *R. pinto* is a distinct species but questioned whether *R. crassicauda* can be regarded as distinct from *R. laticauda*. In our opinion, *R. crassicauda* is probably a junior synonym of *R. laticauda*. Lourenço (2008) rejected the suggestion that *R. crassicauda* may be synonymous with *R. laticauda*, suggesting instead that it might be a subspecies of the latter. Lourenço (2008) also created two new subspecies of *R. crassicauda*. The distinction between *R. laticauda*, *R. crassicauda* and its two subspecies warrants further investigation.

Rhopalurus crassicauda kourouensis Lourenço 2008: French Guiana (Kourou).

Rhopalurus crassicauda parncensis Lourenço 2008: Brazil (Pará).

Rhopalurus garridoi Armas 1974: Cuba (Guantanamo).

Rhopalurus gibarae Teruel 2006: Cuba (Holguín).

Rhopalurus granulimanus Teruel 2006: Cuba (Holguín).

Rhopalurus guanambiensis Lenarducci, et al. 2005: Brazil (Bahia).

Rhopalurus juncus (Herbst 1800): Cuba (Camaguey, Cienfuegos, Ciego de Avila, Granma, Guantanamo, Havana, Holguín, Isla de la Juventud, Las Tunas, Matanzas, Pinar del Rio, Santiago de Cuba, Sancti Spiritus, Villa Clara). Records of this species from Haiti and Venezuela (see, e.g. Fet & Lowe 2000: 220) are probably erroneous (Armas 2001:248).

Rhopalurus lacrau Lourenço & Pinto-da-Rocha 1997: Brazil (Bahia).

Rhopalurus laticauda Thorell 1876: Colombia (Arauca, Boyacá, Casanare, Cesar, Meta, La Guajira, Magdalena, Norte de Santander, Vichada), Venezuela (Amazonas, Anzoátegui, Apure, Aragua, Barinas, Bolívar, Carabobo, Cojedes, D.F., Falcon, Guárico, Lara, Mérida, Miranda, Monagas, Nueva Esparta, Portuguesa, Sucre, Táchira, Vargas, Yaracuy, Zulia).

Rhopalurus melloleitaoi Teruel & Armas 2006: Cuba (Granma).

Rhopalurus pinto Mello-Leitão 1933: Brazil (Roraima), Guyana, ?Venezuela (Bolívar). This species was relegated to a subspecies of *R. laticauda* by Lourenço (1982) until reinstated by Lourenço (2002). Teruel (2006) suggested that it might be a senior synonym of *Rhopalurus piceus* Lourenço & Pinto-da-Rocha 1997 and this was confirmed by Teruel & Tietz (2008). Lourenço (2008) agreed with the recognition of *R. pinto* as a distinct species, but suggested that *R. piceus* may yet prove to be valid. We agree with the decision of Teruel & Tietz (2008).

Rhopalurus princeps (Karsch 1879): Dominican Republic (Azua, Barahona, Baoruco, Independencia, Montecristi, Pedernales, Peralva), Haiti (Département du l'Ouest). Records of this species from Cuba (listed by Fet & Lowe 2000:221) are erroneous.

Rhopalurus rochae Borelli 1910: Brazil (Bahia, Ceará, Paraíba, Pernambuco, Piauí, Rio Grande de Norte, Sergipe*). Borelli (1910) named the species after Francisco Diaz da Rocha, but his original spelling was *rochae*. Fet & Lowe (2000) noted that the correct spelling is *rochai* and changed it accordingly. Although the corrected spelling has been adopted by others (e.g., Teruel 2006:52), we use Borelli's (1910) original spelling.

Troglophorolurus translucidus Lourenço, et al. 2004: Brazil (Bahia). In our opinion, this monotypic genus is a junior synonym of *Rhopalurus*. As twice noted by Lourenço et al. (2004:1153, 1156), when comparing *Troglophorolurus* with *Rhopalurus*: "It may be that all modifications presented by the new troglobitic scorpion are the result of adaptation to a cave dwelling life."

Appendix 2. Material examined for comparison with *Rhopalurus abudi* Armas & Marciano Fondeur, 1987. Specimens are deposited in the following collections: American Museum of Natural History (AMNH), New York, USA, incorporating the Alexis Harington (AH) Collection; Natur-Museum Senckenberg, Frankfurt (SMF), Germany; Zoologisches Museum der Humboldt-Universität, Berlin (ZMB), Germany; Zoologisches Museum der Universität Hamburg (ZMH), Germany. Reference numbers (ESV and LP), provided on labels with the specimens, correspond to entries in the specimen databases of the author with the corresponding initials.

Physoctonus debilis (C.L. Koch, 1840): BRAZIL: Pernambuco: Exu, 5 km N, 4 October 1977, L.J. Vitt, 1 ♀ (AMNH), 18 January 1978, L.J. Vitt & K.E. Streilein, 1 ♀ (AMNH); Exu, 18 km N, 5 March 1977, L.J. Vitt, under leaf of granite on boulder, caatinga habitat, 1 ♀ (AMNH); Fazenda Batente, 13 km E Exu, 10 November 1977, L.J. Vitt & K.E. Streilein, 1 ♀ (AMNH); Fazenda Caterino, 10 km NE Exu, 9 July 1977, L.J. Vitt, 1 ♀ (AMNH), 25 September 1977, L.J. Vitt, 1 ♀ (AMNH).

Rhopalurus acromelas Lutz & Mello, 1922: BRAZIL: Maranhão: Município de Loreto: Santa Barbara, on shore of Rio Parnaíba, June 1962, G. Eiten, 1 ♂ (AMNH). Pernambuco: Exu, 10 km N, 13 March

1977, L.J. Vitt, rocky habitat within thorn scrub forest, 1 ♀, 1 subad. ♀, 4 juv. (AMNH), 14 March 1977, L.J. Vitt, rocky habitat in thorn scrub, 1 ♂, 1 ♀ (AMNH [ESV7532]); Exu, 10 km NE, 28 April 1977, L.J. Vitt, 1 ♂, 1 ♀, 2 subad. ♀, 2 subad., 1 juv. (AMNH), 25 September 1977, L.J. Vitt, 1 ♂, 1 ♀ (AMNH [ESV7244]); Exu, 15 km NE, 14 May 1977, L.J. Vitt, high caatinga, under bark of tree, 1 subad. ♀ (AMNH); Exu, 20 km E, 30 March 1977, L.J. Vitt, 1 juv. ♂ (AMNH); Fazenda Caterino, 10 km NE Exu, 9 July 1977, L.J. Vitt, 1 subad. ♂ (AMNH), 1 August 1977, L.J. Vitt, 1 juv. ♂ (AMNH).

Rhopalurus agamemnon (Herbst, 1800): BRAZIL: *Bahia*: Salvador, February 1972, Weinkelbaum, 1 ♀ (AMNH [ESV7405]).

Rhopalurus bonettii Armas, 1999: DOMINICAN REPUBLIC: *Pedernales Province*: Parque Nacional Jaragua: Cabo Rojo, 17°53'45.2"N, 71°39'35.8"W, 9 July 2004, E.S. Volschenk & J. Huff, 15 m, dry cactus and spiny forest on limestone karst, hand collected at night with blacklights, 3 ♂, 10 ♀, 4 subad., 2 juv. (AMNH [ESV6005]), 1 ♂ (AMNH [ESV7126]), 1 ♂, 1 ♀ (AMNH [ESV7127]), 1 subad. ♂ (AMNH), 1 juv. ♂ (AMNH [LP 3267]); Road to Fondo Paradi, 1.8 km from Highway 44, 17°48.692'N, 71°26.600'W, 12 January 2004, J. Huff, 302 ft, found between rocks, 1 ♀ (AMNH [LP 2471]), 1 ♀ (AMNH [LP 3265]); Track into park, between Manuell Goa and Oviedo, 17°48'41.5"N, 71°26'35.9"W, 9 July 2004, E.S. Volschenk & J. Huff, 83.3 m, deciduous forest and thorny scrub, hand collected from between stones during the day and with blacklights at night, 13 ♂, 7 ♀, 1 subad., 1 juv. (AMNH [ESV6011]), 1 ♂, 1 ♀ (AMNH [ESV7112]), 1 ♂ (AMNH [ESV7129]), 1 juv. (AMNH [LP 3266]).

Rhopalurus caribensis Teruel & Roncallo, 2008: COLOMBIA: *Magdalena Department*: Bahia de Guairaca, Tayrona Park, 31 October 1985, H.-G. Muller, 1 ♀ (SMF 37027); Pozo Colorado, 11 km W Santa Marta, 18–30 April 1968, B. Malkin, 1 ♀, 1 subad., 19 first instars (AMNH); Puente de Los Clavos, 15 km E Pueblo Bello, Sierra Nevada de Santa Marta, 13 June 1968, B. Malkin, 1500 m, 1 subad. ♀ (AMNH); Santa Marta, 29 June–31 July 1966, 2 ♀ (SMF 39120).

Rhopalurus crassicauda Caporiacco, 1947: BRAZIL: *Amazonas*: Rio Branco, Amazonasgebiet, 1912, E. Ule, 1 juv. ♀ (ZMB 14867). *Roraima*: Mt. Roraima, 2 ♂, 1 ♀, 1 subad. (AMNH 29180).

Rhopalurus junceus (Herbst, 1800): CUBA: July 2007, C. Hamilton, 1 juv. (AMNH [LP 7009]); 'Antillen?', 1 ♂, 2 ♀ (ZMB 7370); 'Portorico', Stahl, 2 ♀, 1 juv. (ZMB 7280 [ESV7001]); Gundlach, 2 ♀ (ZMB 2637), 1 ♂, 1 ♀ (ZMB 7380 [ESV7224]), 1 juv. (ZMB, 7343); Arroyo Bermejo, near Fiacoca, 31 May 1967, Kleiderschrank, 1 ♂ (ZMB 31020), 15 June 1967, im zelt. wiese auf sandboden, 1 ♀ (ZMB 31021), June 1967, 1 juv. (ZMB 31022); 1 ♂ (ZMH), Santiago de las Caballeros, P. Thumb, 1936. *Havana Province*: Havana, 1 ♀ (AMNH), April 1941, Dr E. Weiss, 1 ♀, 1 subad. (AMNH). *Holguin Province*: August 2000, Heist, captive bred, 1 juv. (AMNH [LP 1928]); near Baños [Banes], May 1918, 2 ♂ (AMNH); Guardalavaca, 29 March 1993, W. Altmann, captive bred, 1 ♂ (AMNH [LP 1565]); Mountains near Guisa, October 1936, P. Thumb, 1 ♀, 28 juv. (ZMH); Moa, September 1937, P. Thumb, 1 ♂ (ZMH), 1938, P. Thumb, 4 ♀ (ZMH). *Isla de la Juventud Province*: Isle of Pines, 1 ♂ (AMNH). *Pinar del Rio Province*: Guanahacabiles, Akad.-stat. El Beral, December 1967, G. Peters, 1 subad. (ZMB 31023); Sierra de Anafo, 23 February 1947, M. Barro, 2 subad. (AMNH); Vinales Valley, 1940, Osorio, 1 ♀ (AMNH). *Santiago de Cuba Province*: La Socapa, 10 km SW of Santiago de Cuba, 9 April 1999, R. Teruel, 1 ♂ (AMNH), 1 ♀ (AMNH [LP 1509]), 1 juv. ♀ (AMNH [LP 1517]), 1 ♀ (AMNH [LP 1518]); Santiago de Cuba, 1 ♂, 2 juv. (AMNH). *Sancti Spiritus Province*: Trinidad, August 1978, B. Acosta, 1 ♂ (AMNH AH 4514 [ESV7041]).

Rhopalurus lacrau Lourenço & Pinto-da-Rocha, 1997: BRAZIL: *Bahia*: Município Itacaré: Trail between Caves "Lapa do Bode" and "Lapa Escondida," 12°56'9.1"S, 41°3'56.2"W, 21 January 2007, C.I. Mattoni, R. Pinto-da-Rocha & H. Yamaguti, under rocks, 2 ♀ (AMNH), 1 subad. ♀, 4 juv. (AMNH [LP 7637]).

Rhopalurus laticauda Thorell, 1876: 2 ♀ (ZMB 14865); "Mexico," Dr v. Hubl, 1 ♂ (ZMB 14866). VENEZUELA: F. Kummerow, 1 ♂, 1 ♀ (ZMB 8226). San Jose de Guaviare, December 1955, Meden, 1 ♀ (SMF 39252). *Aragua*: Maracay, 1 subad. ♂ (SMF 29208), Fahrenholz, 1 ♂, 1 ♀, 1 subad. (SMF 8876/218). *Bolívar*: Ciudad Bolívar, 20 February 1903, 2 ♀ (ZMH); La Paragua, M.A. de Verde, 1 ♂ (AMNH); Upata, February 1973, A. Bordes, 1 ♀ (AMNH). *Carabobo*: Valencia, F. Kummerow, 29 December 1904, 1 ♀ (ZMB 31024), September 1958, H. Ardel, 2 ♀ (ZMH). *Distrito Federal*: Caracas, March 1999, C. Siederman, 2 ♀, 20 first instars (AMNH [ESV7444]), 2001, C. Siederman, 1 ♂ (AMNH [LP 2462]). *Guarico*: Calabozo and San Fernando de Apure (about halfway between), 30 November 1967, M.A. de Verde, 1 ♀ (AMNH); 'Hato Masaguarat,' 45 km S Calabozo, 7 April 1978, Y. Lubin, 1 ♂ (AMNH [ESV7816]). *Mérida*: Mérida, 2 ♂, 3 ♀ (SMF 5712/27). *Miranda*: Guatire, 29 April 2004, R.C. West, under rocks, dry forest, 1 ♂ (AMNH [LP 2845]), 1 ♀ (AMNH); Hda. Santa Rosa, 3 km N Guatire, 10 January 1973, M.A. González-Sponga, 450 m, 1 ♂, 1 ♀, 2 juv. (AMNH). *Nueva Esparta*: Isla Margarita, N of Peninsula de Macanao, 11°02.618'N, 64°21.542'E, 4 September 2005, S. Huber, 1 ♀ (AMNH [LP 4221]). *Trujillo*: Valera region, N, October 2005, S.E. Bazo Abreu, 1 ♀ (AMNH [LP 5504]), 1 ♀ (AMNH [LP 5505]).

Rhopalurus pintoii Mello-Leitão, 1933: GUYANA: *Roraima Province*: Rununui region, SW Guyana, near Venezuelan border, ex A. Tietz, March 2008, 1 juv. ♂ (AMNH [LP 8278]).

Rhopalurus princeps (Karsch, 1879): DOMINICAN REPUBLIC: *Independencia Province*: Isla Cabritos, 18°30.019'N, 71°43.228'W, 7 January 2004, J. Huff, 110 ft, under rock, coral, 1 ♂, 1 ♀, 16 juv. (AMNH), 5 ♂, 3 ♀, 3 subad., 1 juv. (AMNH), 3 juv. (AMNH [LP 2470]), 1 subad., 2 juv. (AMNH [LP 3260]); Ranger station for Parque Nacional Isla Cabritos, 18°33'45"N, 71°41'50"W, 8 July 2004, E.S. Volschenk & J. Huff, -19 m, dry forest, hand collected from under stones and logs, and with blacklights, 3 ♂, 7 ♀, 5 subad., 2 juv. (AMNH [ESV6006]), 1 subad. ♂ (AMNH), 1 subad. (AMNH [LP 3264]); Parque Nacional Isla Cabritos, behind Ranger Station, 18.56287°N, 71.69762°W, 8 August 2005, L. Esposito, -23 m, mixed dry forest with succulents, UV detection, 35°C, 2 ♂, 8 ♀, 1 subad. ♀, 32 first instars (AMNH), 2 ♂, 1 subad. ♀ (AMNH), 1 ♂ (AMNH [LP 5102]); Parque Nacional Sierra de Baoruco, road between Rabo de Gato and Duverge, 18°19'38"N, 71°33'55"W, 7 July 2004, E.S. Volschenk & J. Huff, 447 m, arid thorny scrub, hand collected from under stones and in dead and dry agaves, 3 ♂, 3 ♀, 3 juv. (AMNH [ESV6033]), 1 juv. (AMNH), 1 ♀ (AMNH [LP 3263]); Puerto Escondido, Sierra de Baoruco, 18°19.762'N, 71°33.502'W, 6 January 2004, J. Huff, 1592 ft, under dead agave, 1 ♂, 3 ♀, 1 juv. (AMNH), 1 juv. (AMNH [LP 3261]); Road to Puerto Escondido, 18°20.376'N, 71°33.345'W, 6 January 2004, J. Huff, 1388 ft, under rocks in gravel quarry, 1 ♀ (AMNH), 1 juv. (AMNH [LP 3262]). *Pedernales Province*: Manuel Goja, 3.9 km N, 9 May 1998, D. Huber, 1 ♂ (AMNH [LP 1566]); Oviedo to Pedernales, 11.5 km N, 8 May 1998, D. Huber, 1 ♂ (AMNH [LP 1516]). HAITI: *Département de l'Ouest*: Port-au-Prince, Ehrenberg, holotype ♂ (ZMB 116).

Rhopalurus rochae Borelli, 1910: BRAZIL: *Bahia*: Município Ceraima: Guanambi, 7 km S, 14°17'5.6"S, 42°47'2.2"W, 24 January 2007, C. Mattoni, R. Pinto-da-Rocha & H. Yamaguti, 533 m, UV sampling, modified savanna, cloudy and raining, 1 juv. (AMNH [LP 7638]); Fazenda du Fabiano, 8 km NE Guanambi, 14°10'17.6"S, 42°43'56.4"W, 24 January 2007, C. Mattoni, R. Pinto-da-Rocha & H. Yamaguti, 539 m, under rocks, rocky hill and surrounds, open savanna modified, 1 ♂, 2 juv. (AMNH [LP 7639]), 1 ♀ (AMNH); Guanambi, 16 km SE, 14°17'19"S, 42°41'31.1"W, 25 January 2007, C. Mattoni, R. Pinto-da-Rocha, H. Yamaguti, 559 m, UV sampling and under leaf litter, banana plantation and surrounds, 1 juv. (AMNH [LP 7655]). *Paraíba*: Soledade, 07°02.118'S, 36°27.311'W, 16 March 1999, A. Kury & A. Giupponi, 575 m, 1 ♂ (AMNH [LP 1581]), 1 ♀ (AMNH [LP 1582]), 1 ♂ (AMNH [LP 1775]). *Pernambuco*: Escola

Aquicola, Exu, 30 March 1977, L.J. Vitt, caatinga, 1 ♂ (AMNH [ESV7248]), 27 June 1977, L.J. Vitt, 1 ♂ (AMNH); Exu, 3 km NW, 10 March 1977, L.J. Vitt, 2 ♂, 1 ♀, 3 juv. (AMNH); Exu, 3 km W, 30 May 1977, L.J. Vitt, 2 ♂, 4 ♀, 4 juv. (AMNH), 1 June 1977, L.J. Vitt, 1 ♀ (AMNH); Exu, 5 km N, 6 April 1977, L.J. Vitt, caatinga, 1 ♂, 1 juv. (AMNH), 18 January 1978, L.J. Vitt & K.E. Streilein, 1 juv. (AMNH); Exu, 5 km E, 8 May 1977, L.J. Vitt, 1 juv. (AMNH); Exu, 6 km N, 15 March 1977, L.J. Vitt, open fields (cotton), under fallen logs, 1 ♀, 1 juv. ♂ (AMNH); Exu, 6 km NE, 16 March 1977, L.J. Vitt, under rock on larger rock, caatinga habitat, 1 ♀, 49 first instars (AMNH); Exu, 18 km E, 5 March 1977, L.J. Vitt, under leaf of

granite on boulder, caatinga habitat, 1 ♀, 29 first instars (AMNH), 1 ♀, 39 first instars (AMNH [ESV7210]); Exu, 20 km E, 30 March 1977, J.L. Vitt, 1 ♂, 1 ♀ (AMNH [ESV7625]); Fazenda Batente, 5 km NE Exu, 29 March 1977, L.J. Vitt, 1 juv. (AMNH); Fazenda Caterino, 10 km NE Exu, 1 August 1977, L.J. Vitt, 2 ♂, 3 juv. (AMNH), 5 ♂, 3 ♀ (AMNH); Fazenda Chelonia, 8 km S Exu, 28 July 1977, L.J. Vitt, 2 juv. (AMNH); Fazenda Guarani, 3 km N Exu, 14 July 1977, L.J. Vitt, 1 ♂, 3 ♀, 1 subad. 3 juv. (AMNH); Fazenda Guarani, 5 km N Exu, 29 July 1977, L.J. Vitt, 1 ♀, 3 juv. (AMNH), 19 February 1978, L.J. Vitt, 1 ♀ (AMNH). *Sergipe*: Municipio Lagarto: near Genipapo, July 1982, O.F. Francke, 1 ♂, 2 ♀ (AMNH).

Wolf spiders of the Pacific region: the genus *Zoica* (Araneae, Lycosidae)

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Abstract. The wolf spider genus *Zoica* Simon 1898 is currently known only from the Indo-Australasian region, including India in the west to northern Western Australia and Papua New Guinea in the east. Here we extend the known distribution of the genus into the Pacific region by describing two new species, *Z. carolinensis* new species from the Caroline Islands, Federated States of Micronesia, and *Z. pacifica* new species from the Republic of the Marshall Islands.

Keywords: Zoicinae, taxonomy, Marshall Islands, Caroline Islands, Micronesia

Our knowledge of the wolf spider fauna of the Pacific is only fragmentary. The fauna of New Caledonia and Vanuatu (e.g., Berland 1924, 1938) and Hawaii (Karsch 1880; Simon 1899, 1900; Gertsch 1973) have received some attention, although most species were described in the late 1800s to early 1900s. Modern taxonomic descriptions that allow accurate species identifications do not exist and, in most cases, identification of species is impossible without recourse to type material. In addition, generic classification of most Pacific wolf spider species does not follow phylogenetic guidelines but is based on perceived similarities of species with genera originally described from the Northern Hemisphere, mainly Europe, where most arachnologists were then based.

The Pacific islands wolf spider fauna currently includes representatives of three subfamilies (cf. Dondale 1986; Murphy et al. 2006). The Lycosinae Sundevall 1833, which include genera such as *Lycosa* Latreille 1804, *Hogna* Simon 1885, *Adelocosa* Gertsch 1973 and *Venatrix* Roewer 1960, dominate the wolf spider fauna of the Pacific islands both in diversity and local abundance (e.g., Simon 1899, 1900; Framenau 2006, unpublished data); however, many Pacific lycosines are clearly misplaced at the genus level. The Artoriinae Framenau 2007 are represented by *Artoria* Thorell 1877, *Lycosella* Thorell 1890, and *Syroloma* Simon 1900 and are currently reported from New Caledonia, Vanuatu, Hawaii, Samoa, and French Polynesia (e.g., Simon 1900; Berland 1929, 1934; Framenau 2007). Two species of *Venonia* Thorell 1894 in the subfamily Venoniinae Lehtinen & Hippa 1979 have been reported from Palau (Yoo & Framenau 2006). It appears that the lycosid fauna of the Pacific has strong affinities with Australia and Southeast Asia as, for example, Venoniinae and Artoriinae do not occur in the Americas to the east.

The wolf spider subfamily Zoicinae Lehtinen & Hippa 1979 has so far not been reported from the Pacific. Dondale (1986) synonymized this subfamily with the Venoniinae; however, this synonymy was rejected & the subfamily revalidated in a recent revision of *Venonia* (Yoo & Framenau 2006). Zoicinae include five genera from the Indo-Australasian region: *Zoica* Simon 1898, *Lysania* Thorell 1890, *Zantheres* Thorell 1887, *Margonia* Hippa & Lehtinen 1983, and *Shapna* Hippa & Lehtinen 1983 (Hippa & Lehtinen 1983; Yoo & Framenau

2006). Lehtinen & Hippa (1979; p. 2, table 1) proposed a number of diagnostic characters for the Zoicinae, two of which, regarding the male pedipalp, clearly represent synapomorphies for the subfamily: the lack of a median (= tegular) apophysis and the distal origin of the embolus.

With a body length of generally not more than 2.5 mm, members of the genus *Zoica* are amongst the smallest of all wolf spiders. The genus, with *Z. parvula* (Thorell 1895) as type species, was established by Simon (1898) replacing *Zobia* Thorell 1895, preoccupied by *Zobia* Saalmueller 1891, a butterfly genus. *Zoica* was revised by Lehtinen & Hippa (1979) who reported six species from India and Sri Lanka in the West, throughout Southeast Asia (Myanmar, Malaysia, Thailand, Indonesia) including Papua New Guinea to the east. More recently, a single species of *Zoica* was described from Bhutan (Buchar 1997). The genus also occurs in northern Western Australia and the tropical parts of the Northern Territory and Queensland (Australia) (McKay 1979; Platnick 2008; VWF unpublished data).

This study reports the subfamily Zoicinae for the first time from the Pacific region by describing two new species of *Zoica* from the Federated States of Micronesia and the Republic of the Marshall Islands (see Fig. 13).

METHODS

A large collection of spiders ("BB" collection, presently housed at Southern Illinois University, Carbondale, Illinois, USA) was made by J.W. Berry, E.R. Berry, and J.A. Beatty in a series of collecting trips into the Pacific region: Marshall Islands (1968, three months; 1969, 3 mo); Palau (1973, 6 mo); Guam, Yap, Truk (= Chuuk), Ponape (= Pohnpei), Taiwan (1973, 1–2 wk each); Yap (1980, 6 mo); Marquesas Islands, Tuamotu, Society, Cook and Fiji Islands (1987 & 2004, 6 mo in total); Cook Islands (2002, 6 wk); and the Hawaiian islands (1995, 1997 & 1998, 3 mo in total). The collections reported herein are from the 1973 trip to the Caroline Islands, and 1968, 1969, and 1980 visits to the Marshall Islands. Spiders were generally hand collected.

Descriptions are based on specimens preserved in 70% ethanol. Female epigyna were prepared for examination by submersion in 10% KOH for 10 min. For clarity, the

illustrations of male pedipalps and female epigyna omit setae. The morphological nomenclature follows Lehtinen & Hippa (1979), Hippa & Lehtinen (1983) and Yoo & Framenau (2006). Lehtinen & Hippa (1979) introduced the term "truncus" in the Lycosidae for a sclerite of the male pedipalp that originates basally between the subtegulum and the tegulum in replacement of Kronstedt's (1975) "terminal part" [erroneously termed "terminal apophysis" in Lehtinen & Hippa (1979: p. 3)]. Consequently, they also called the distinct lateral apophysis originating at the truncus, "lateral truncal apophysis" but replaced this term later (Hippa & Lehtinen 1983) with "lateral apophysis" as this structure is referred to here (see Figs. 5, 9). The term "truncus" for the apical section of the male bulb has not been used in the lycosid morphology since Lehtinen & Hippa's (1979) and Hippa & Lehtinen's (1983) initial studies and was referred to as "embolic division" in Yoo & Framenau (2006). All measurements are given in millimeters (mm).

Images were taken with a Leica DFC500 digital camera that was attached to a Leica MZ16A stereomicroscope. Photographs were taken in different focal planes (ca. 10–15 images) and combined with the Leica Application Suite version 2.5.0R1.

Abbreviations.—*Collections:* BB, Berry-Beatty collection, presently at Southern Illinois University; BPBM, Bernice P. Bishop Museum, Honolulu (Hawai'i); WAM, Western Australian Museum (Perth). *Morphology:* AE (AME, ALE), anterior (median, lateral) eyes; AL (AW), abdomen length (width); CL (CW), carapace length (width); PE (PME, PLE), posterior (median, lateral) eyes; TL, total length.

SYSTEMATICS

Family Lycosidae Sundevall 1833

Subfamily Zoicinae Lehtinen & Hippa 1979

Zoica Simon 1898

Zobia Thorell 1895:53–54 (preoccupied by the butterfly genus *Zobia* Saalmüller 1891).

Zoica Simon 1898:248 (replacement name for *Zobia* Thorell 1895).

Type species.—*Zobia parvula* Thorell 1895, by original designation (Thorell 1895).

Diagnosis.—Within the Zoicinae, *Zoica* is most closely related to *Lysania*, based on the overall structure of the male pedipalp and absence of glistening setae on the abdomen (present in all other genera of the subfamily) (Hippa & Lehtinen 1983). However, *Zoica* is generally smaller, (TL 1.5–2.3) than *Lysania* (TL 2.2–3.0), although sizes may overlap. The cephalic area of *Zoica* is gently sloping laterally, whereas it is steep in *Lysania* (and in all other genera of the Zoicinae). *Lysania* show distinct color patterns of white anterolateral abdominal bands and light annulations of the legs, whereas members of *Zoica* are uniformly yellow-brown to brown. In addition, *Lysania* build horizontal, sheet-like webs, whereas *Zoica* are vagrant (Lehtinen & Hippa 1979).

Description.—Minute to small spiders (TL 1.5–2.3); uniformly yellow-brown to dark grey; cephalic area gradually sloping laterally; row of AE recurved to slightly procurved; PME never more than half their diameter apart; leg formula IV > I > II > III; male pedipalp without articulated tegular

apophysis; lateral apophysis present; embolus a thin, curved spine and mostly covered by tegulum in ventral view; epigynum variable, often protruding scape-like posteriorly.

The gently sloping margins of the cephalic area, small size and the lack of a distinct color pattern are here considered synapomorphies for *Zoica*. Lehtinen & Hippa (1979) reported a dorsal abdominal scutum in males, which we cannot confirm for the species described here or for any of the three species known from Australia (McKay 1979; VWF unpublished data).

Zoica carolinensis new species

(Figs. 1, 2, 5–8, 13)

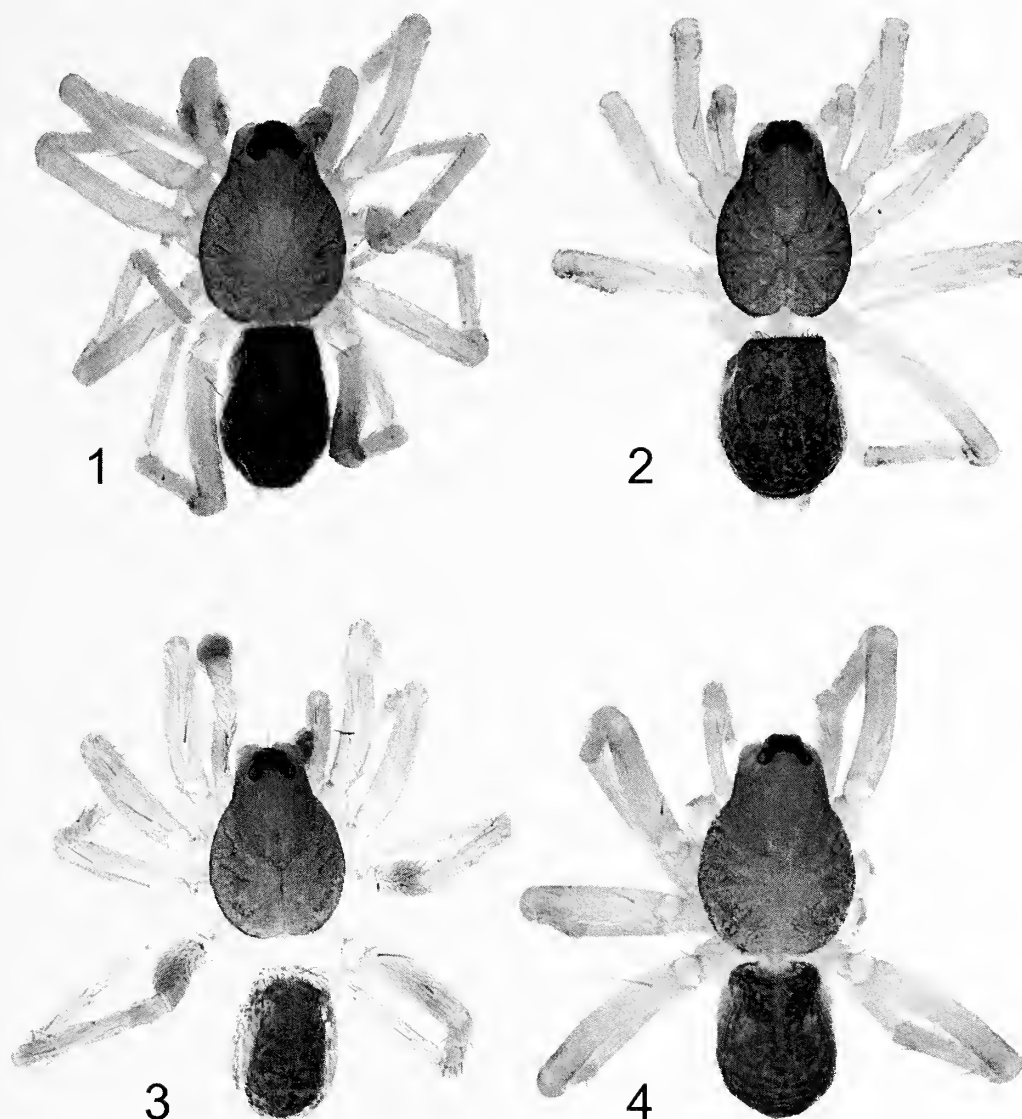
Types.—Holotype male, Federated States of Micronesia, Caroline Islands, Ponape (= Pohnpei), E of Kolonia, 6°57'50"S, 158°12'30"E, 7 June 1973 J.A. Beatty, J.W. Berry (BPBM); paratype female, data as holotype (BPBM).

Other material examined.—FEDERATED STATES OF MICRONESIA: Caroline Islands: 1 female, Pohnpei, E of Kolonia, 6°57'N, 158°15'E, 7 June 1973; 2 males, 9 females, 2 females with eggsac, 5 juveniles, Pohnpei, Sokehs Island, 6°57'N, 158°11'E, 8 June 1973, J.A. Beatty, J.W. Berry (BB); 1 male, 3 females, same data (WAM T80644).

Diagnosis.—*Zoica carolinensis* is similar to *Z. wauensis* Lehtinen & Hippa 1979 from Papua New Guinea as illustrated in Lehtinen & Hippa (1979), in particular in regard to the structure of the male pedipalp. However, the basal part of the embolus is more exposed in *Z. wauensis* and the median tegular lobe is narrower and longer than that in *Z. carolinensis*. Both species differ considerably in the shape of the female epigynum, which is highly prominent in *Z. wauensis* (see Lehtinen & Hippa 1979), but is flat in *Z. carolinensis*. Unfortunately, we were not able to compare specimens of both species as material of *Z. wauensis*, including the type material, could not be located in the Zoological Museum, University of Turku, Finland, where it is supposed to be housed (S. Kopponen, personal communication to VWF). *Zoica carolinensis* differs from *Z. pacifica*, the second species described here, by the presence of a median tegular lobe in the male pedipalp (absent in *Z. pacifica*) and the lack of a posterior lip of the epigynum (present in *Z. pacifica*).

Description.—*Male (based on holotype):* Carapace: dorsal profile straight in lateral view; uniformly yellow-brown with gray pigmentation, centrally somewhat lighter, black around eyes (Fig. 1). Eyes: row of AE as wide as row of PME; row of AE very slightly procurved. Sternum: yellow, with some gray pigmentation marginally; brown macrosetae mainly marginally. Labium: yellow-brown. Chelicerae: yellow-brown with indistinct gray pigmentation, basally slightly darker; few whitish setae. Pedipalp (Figs. 5, 6): lateral apophysis tapering and bent dorsally at tip; embolus covered by terminal apophysis both of which are behind median tegular lobe (Fig. 5). Abdomen: yellow-brown with dense olive-gray pigmentation (Fig. 1); venter yellow. Legs: leg formula IV > I > II > III; uniformly yellow; spination of leg I: femur: 2 dorsal (only 1 on right leg), 1 apicoprolateral; tibia: 2 ventral pairs; metatarsus: 3 ventral pairs.

Female (based on paratype): In all details like male (Fig. 2), except row of AE straight. Epigynum (Figs. 7, 8): ventral view:



Figures 1–4.—*Zoica* spp. 1. *Z. carolinensis*, holotype male from Ponape, E of Kolonia (Caroline Islands, Micronesia) (BPBM); 2. *Z. carolinensis*, paratype female from Ponape, E of Kolonia (Caroline Islands, Federated States of Micronesia) (BPBM); 3. *Z. pacifica*, holotype male from Majuro Islet (Majuro Atoll, Marshall Islands) (BPBM); 4. *Z. pacifica*, female from Majuro Islet (Majuro Atoll, Marshall Islands) (BPBM). TL: (1) 1.63 mm; (2) 1.77 mm; (3) 1.92 mm; (4) 1.84 mm.

weakly sclerotized with narrow posterior openings (Fig. 7); dorsal view: fertilization ducts form slightly bent tubes (Fig. 8).

Measurements: Male holotype (female paratype): TL 1.63 (1.77), CL 0.90 (0.92), CW 0.65 (0.65). Eyes: AME 0.02 (0.03), ALE 0.03 (0.04), PME 0.06 (0.08), PLE 0.06 (0.06). Row of eyes: AE 0.15 (0.17), PME 0.14 (0.17), PLE 0.24 (0.26). Sternum (length/width) 0.54/0.42 (0.46/0.44). Labium (length/width) 0.10/0.12 (0.15/0.10). AL 0.79 (0.81), AW 0.73 (0.63). Legs: lengths of segments (femur, patella/tibia, metatarsus, tarsus = total length): Pedipalp 0.38, 0.31, -, 0.36 = 1.06; leg I 0.63, 0.77, 0.48, 0.36 = 2.25; leg II 0.60, 0.67, 0.44, 0.35 = 2.05; leg III 0.56, 0.60, 0.48, 0.33 = 1.96; leg IV 0.77, 0.90, 0.73, 0.40 = 2.80 (Pedipalp 0.31, 0.38, -, 0.32 = 1.01; leg I 0.69, 0.83, 0.48, 0.36 = 2.36; leg II 0.65, 0.69, 0.44, 0.35 = 2.13; leg III 0.60, 0.63, 0.46, 0.33 = 2.02; leg IV 0.79, 1.02, 0.69, 0.38 = 2.88).

Variation: ♂ (♀) (range, mean \pm SD): TL 1.61–1.82, 1.73 \pm 0.11; CL 0.88–0.96, 0.92 \pm 0.04; CW 0.63–0.69, 0.67 \pm 0.03; n = 3 (TL 1.73–2.28, 2.00 \pm 0.17; CL 0.90–1.15, 1.00 \pm 0.07; CW 0.65–0.84, 0.75 \pm 0.05; n = 12).

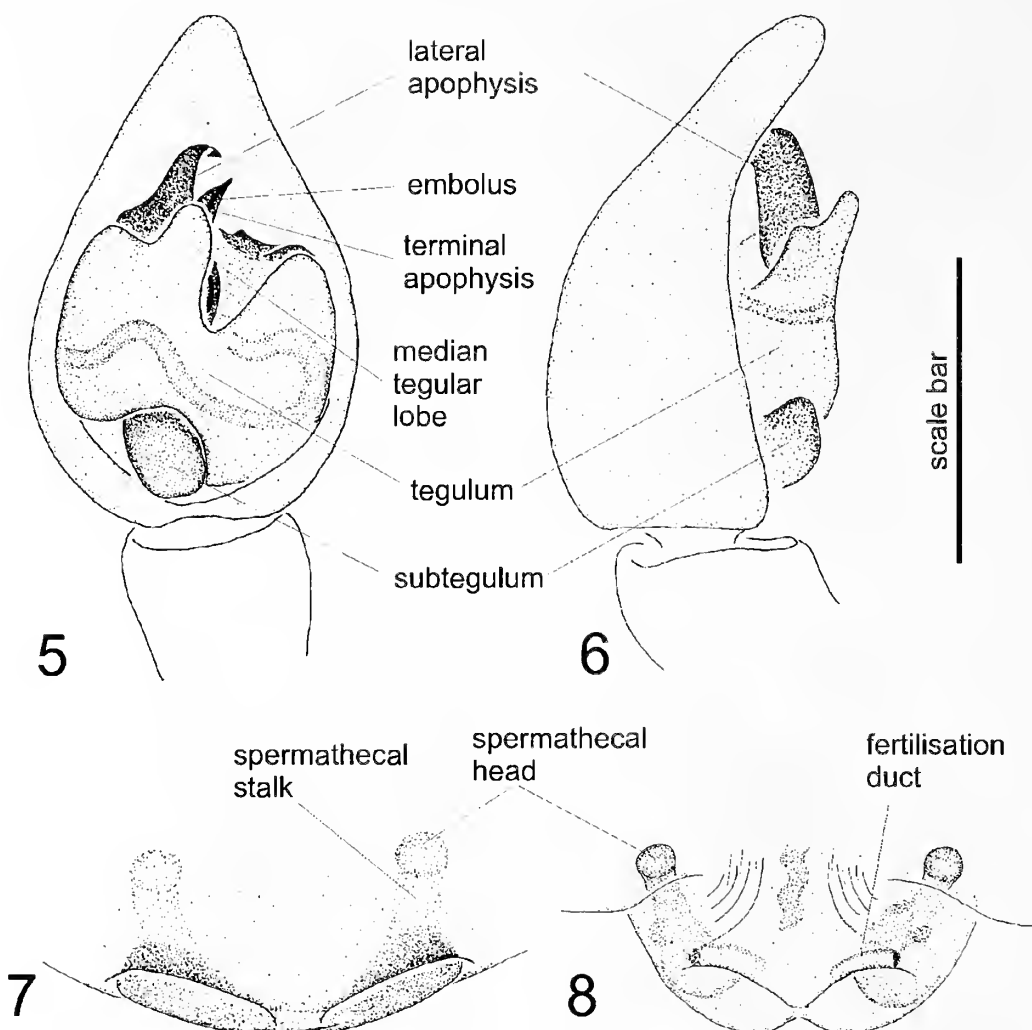
Etymology.—The specific epithet is an adjective derived from the Caroline Islands, where the species is found.

Distribution.—Known only from Ponape (= Pohnpei) in the Caroline Islands, Federated States of Micronesia (Fig. 13).

Zoica pacifica new species
(Figs. 3, 4, 9–13)

Types.—Holotype male, Republic of the Marshall Islands, Majuro Atoll, Majuro Islet, 7°05'N, 171°08'E, 2 August 1969, J.W. Berry, breadfruit/coconut litter (BPBM); paratype female, same data as holotype (BPBM).

Other material examined.—REPUBLIC OF THE MARSHALL ISLANDS: Majuro Atoll: 1 male, 3 females, 5



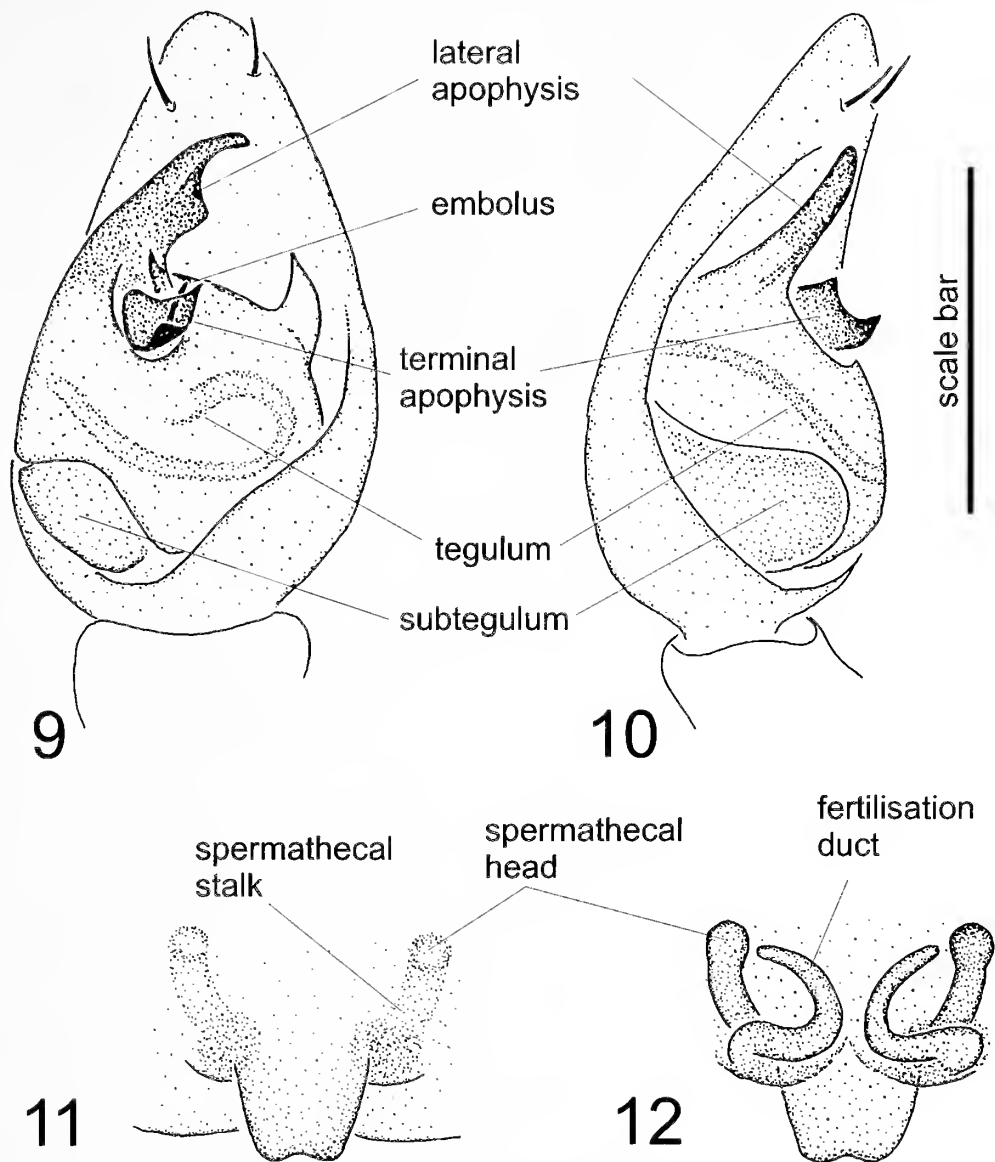
Figures 5–8.—*Zoica carolinensis* new species. Male holotype and female paratype from Ponape, E of Kolonia (Caroline Islands, Federated States of Micronesia) (BPBM). 5. Left pedipalp, ventral; 6. Left pedipalp, retrolateral; 7. Epigynum, ventral view; 8. Epigynum, dorsal view. Scale bars: (5, 6) 0.26 mm; (7, 8) 0.17 mm.

juveniles, 7°07'N, 171°21'E, 30 July 1969, J.W. Berry, grassy meadow (BB); 1 male, 2 females, 4 juveniles, Arniel Islet, 7°06'N, 171°22'E, 1 August 1969, J.W. Berry, grassy area in coconut forest, litter (BB); 1 male, 2 females, 5 juveniles, Dalap Islet, 7°06'N, 171°22'E, 1 August 1969, J.W. Berry, coconut/pandanus litter (BB); 1 male, 2 females, 5 juveniles, Long Island, 6 mi from Laura, 7°05'N, 171°08'E, 24 March 1980, J.A. Beatty, under coconut husks (BPBM); 1 female, 1 juvenile, Long Island, 6 mi from Laura, 7°05'N, 171°08'E, 24 March 1980, J.A. Beatty, from dead coconut leaves (BPBM); 2 females, 5 juveniles, Majuro Islet, 7°05'N, 171°08'E, 2 August 1969, J.W. Berry, breadfruit/coconut litter (BB); 3 females, Majuro Village, 7°06'N, 171°22'E, 24 July 1968, J.W. Berry, wet tropical forest, litter (BB); 1 female, 2 juveniles, Uotjaa Islet, 7°07'N, 171°21'E, 26 July 1968, J.W. Berry, *Scaevola* litter (BPBM); 2 females, 3 juveniles, Uotjaa Islet, 7°07'N, 171°21'E, 26 July 1968, J.W. Berry, coconut litter (BPBM); 2 females, 1 juvenile, Uotjaa Islet, 7°07'N, 171°21'E, 26 July 1968, J.W. Berry, grass litter (BB); 6 females, 6 juveniles, Uotjaa Islet, 7°07'N, 171°21'E, 25 July 1968, J.W. Berry, under coconut litter (BB).

Diagnosis.—*Zoica pacifica* differs from all other species of *Zoica* by the absence of a median tegular lobe in the male pedipalp and the presence of a long posterior lip of the female epigynum.

Description.—*Male (based on holotype)*: Carapace: dorsal profile straight in lateral view; uniformly yellow-brown with gray pigmentation, black around eyes (Fig. 3); light-brown macrosetae around eyes, one large bristle that is bent dorsally centrally below AME, two macrosetae below ALE. Eyes: row of AE as wide as row of PME; row of AE straight. Sternum: long yellow-brown macrosetae mainly marginally. Labium: yellow-brown. Chelicerae: yellow-brown. Pedipalp (Figs. 9, 10): cymbium tip with two ventral macrosetae, lateral apophysis with mesal protrusion (Fig. 9); terminal apophysis with two round lobes and a pointed tip. Abdomen: yellow-brown with dense olive-gray pigmentation (Fig. 3); venter yellow. Legs: leg formula IV > I > II > III; uniformly yellow; spination of leg I: femur: 2 dorsal (only 1 on right leg), 1 apicoprolateral; tibia: 2 ventral pairs; metatarsus: 1 ventral.

Female (based on paratype): In all details like male (Fig. 4), except leg spination: femur: 2 dorsal, 1 apicoprolateral; tibia: 2



Figures 9–12.—*Zoica pacifica* new species. Male holotype and female paratype from Majuro Islet (Majuro Atoll, Marshall Islands) (BPBM). 9, Left pedipalp, ventral; 10, Left pedipalp, retrolateral; 11, Epigynum, ventral view; 12, Epigynum, dorsal view. Scale bars: (9, 10) 0.20 mm; (11, 12) 0.19 mm.

ventral pairs; metatarsus: 3 ventral pairs. Epigynum (Figs. 11, 12): ventral view: weakly sclerotized with long posterior lip (Fig. 11); dorsal view: spermathecal heads slightly wider than spermathecal stalks, fertilization ducts long and curved (Fig. 12).

Measurements: Male holotype (female paratype): TL 1.92 (1.84), CL 0.98 (1.00), CW 0.71 (0.73). Eyes: AME 0.02 (0.03), ALE 0.03 (0.03), PME 0.07 (0.08), PLE 0.06 (0.07). Row of eyes: AE 0.16 (0.17), PME 0.16 (0.17), PLE 0.25 (0.27). Sternum (length/width) 0.46/0.44 (0.54/0.48). Labium (length/width) 0.12/0.16 (0.12/0.16). AL 0.79 (1.02), AW 0.56 (0.65). Legs: lengths of segments (femur, patella/tibia, metatarsus, tarsus = total length): Pedipalp 0.38, 0.34, -, 0.36 = 1.09; leg I 0.71, 0.81, 0.54, 0.40 = 2.46; leg II 0.69, 0.75, 0.50, 0.35 = 2.28; leg III 0.63, 0.69, 0.52, 0.33 = 2.17; leg IV 0.83, 1.00, 0.75, 0.42 = 3.00 (Pedipalp 0.29, 0.34, -, 0.31 = 0.94; leg I 0.71, 0.81, 0.50, 0.38 = 2.40; leg II 0.65, 0.75, 0.46, 0.36 =

2.23; leg III 0.63, 0.69, 0.48, 0.35 = 2.15; leg IV 0.81, 1.06, 0.73, 0.44 = 3.03).

Variation: ♂ (♀) (range, mean \pm SD): TL 1.65–1.92, 1.76 \pm 0.11; CL 0.90–0.98, 0.94 \pm 0.04; CW 0.65–0.71, 0.68 \pm 0.03; n = 4 (TL 1.77–2.30, 2.03 \pm 0.18; CL 0.92–1.11, 1.02 \pm 0.05; CW 0.69–0.81, 0.75 \pm 0.03; n = 12).

Etymology.—The specific epithet is an adjective derived from *pacificus* (Latin – peaceful) and refers to the Pacific region, where the species is found.

Distribution.—Only known from Majuro Atoll in the Republic of the Marshall Islands (Fig. 13).

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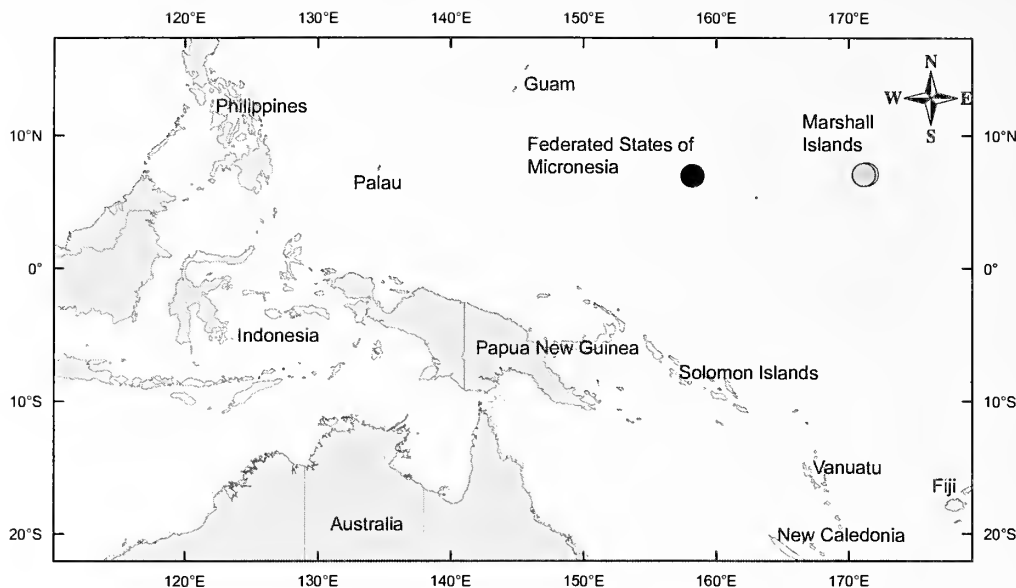


Figure 13.—Records of *Zoica carolinensis* new species (black circle) and *Zoica pacifica* new species (gray circle).

funds for the work in the Marshall Islands. Two travel grants from the Indiana Academy of Science to JWB were of material assistance. Elizabeth Ramsey Berry's contribution to all phases of the fieldwork in the Pacific and at home have been invaluable. The staff at the Bishop Museum, Honolulu, has been of assistance in many ways over a period of decades. This study was compiled while VWF received funds through the Australian Biological Resources Study (ABRS) to Mark Harvey (Western Australian Museum) and Andy Austin (The University of Adelaide) for a revision of the wolf spider fauna of Australia (2002–2005) and to VWF and Nikolaj Scharff (University of Copenhagen) for a revision of the orb-weaving spider fauna (Araneinae) of Australia. The senior author acknowledges, in particular, the support of his mentor Mark Harvey during studies at the Western Australian Museum.

LITERATURE CITED

- Berland, L. 1924. Araignées de la Nouvelle-Calédonie et des Iles Loyalty. *Nova Caledonia, Zoologie* 3:159–255.
- Berland, L. 1929. Araignées (Araneida). Pp. 35–78. *In* *Insects of Samoa and Other Samoan Terrestrial Arthropoda*. British Museum of Natural History, London.
- Berland, L. 1934. Araignées de Polynésie. *Annales de la Société Entomologique de France* 103:321–336.
- Berland, L. 1938. Araignées des Nouvelles-Hébrides. *Annales de la Société Entomologique de France* 107:121–190.
- Buchar, J. 1997. Lycosidae aus Bhutan. I. Venoniinae und Lycosinae (Arachnida: Araneae). *Entomologica Basiliensia* 20:5–32.
- Dondale, C.D. 1986. The subfamilies of wolf spiders (Araneae: Lycosidae). *Actas X Congreso Internacional de Aracnología*, Jaca, España 1:327–332.
- Framenau, V.W. 2006. The wolf spider genus *Veuatrix* Roewer: new species, synonymies and generic transfers (Araneae, Lycosidae). *Records of the Western Australian Museum* 23:145–166.
- Framenau, V.W. 2007. Revision of the new Australian genus *Artoriopsis* in a new subfamily of wolf spiders, Artoriinae (Araneae: Lycosidae). *Zootaxa* 1391:1–34.
- Gertsch, W.J. 1973. The cavernicolous fauna of Hawaiian lava tubes, 3. Araneae (spiders). *Pacific Insects* 15:163–180.
- Hippa, H. & P.T. Lehtinen. 1983. The *zautheres* group of Zoicinae (Araneae, Lycosidae) and a relimitation of the subfamily. *Annales Zoologici Fennici* 20:151–156.
- Karsch, F. 1880. Mittheilung über die von Herrn Dr. O. Finsch während seiner polynesischen Reise gesammelten Myriapoden und Arachniden. *Sitzungsberichte der Gesellschaft naturforschender Freunde Berlin* 5:77–83.
- Kronstedt, T. 1975. Studies on species of Holarctic *Pardosa* groups (Araneae, Lycosidae). I. *Zoologica Scripta* 4:217–228.
- Lehtinen, P.T. & H. Hippa. 1979. Spiders of the Oriental-Australian region. I. Lycosidae: Venoniinae and Zoicinae. *Annales Zoologici Fennici* 16:1–22.
- McKay, R.J. 1979. The wolf spiders of Australia (Araneae: Lycosidae): 10. A new species of the genus *Flanona* Simon. *Memoirs of the Queensland Museum* 19:231–235.
- Murphy, N.P., V.W. Framenau, S.C. Donnellan, M.S. Harvey, Y.C. Park & A.D. Austin. 2006. Phylogenetic reconstruction of the wolf spiders (Araneae: Lycosidae) using sequences from the 12S rRNA, 28S rRNA, and NADH1 genes: implications for classification, biogeography, and the evolution of web building behavior. *Molecular Phylogenetics and Evolution* 38:583–602.
- Platnick, N.I. 2008. The World Spider Catalog, Version 9.0. American Museum of Natural History, New York. Online at <http://research.amnh.org/entomology/spiders/catalog/INTRO1.html> (Accessed October 2008).
- Simon, E. 1898. *Histoire Naturelle des Araignées*, 2. Roret, Paris. Pp. 193–380.
- Simon, E. 1899. Ergebnisse einer Reise nach dem Pacific (Schauinsland 1896–1897). *Arachnoideen. Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere* 12:411–437.
- Simon, E. 1900. *Arachnida. Fauna Hawaiiensis, or the zoology of the Sandwich Isles: being results of the explorations instituted by the Royal Society of London promoting natural knowledge and the British Association for the Advancement of Science and carried on with the assistance of those bodies and of the Trustees of the Bernice Pauahi Bishop Museum at Honolulu*. Cambridge

- University Press, Cambridge, UK. Volume 2 Part 5 (ad part): 443–519.
- Thorell, T. 1895. Descriptive Catalogue of the Spiders of Burma, Based Upon the Collection Made by Eugene W. Oates and Preserved in the British Museum. British Museum of Natural History, London. 397 pp.
- Yoo, J.-S. & V.W. Framenau. 2006. Systematics and biogeography of the sheet-web building wolf spider genus *Venomia* (Araneae: Lycosidae). *Invertebrate Systematics* 20:675–712.

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Plant nectar increases survival, molting, and foraging in two foliage wandering spiders

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Abstract. We predicted that because plant nectar is high in energy, it is likely to provide multiple benefits to spiders that spend a substantial amount of energy foraging. In three laboratory experiments, we tested the effects of dietary extrafloral nectar on the survival, molting, and activity of two foliage wanderers, *Cheiracanthium mildei* L. Koch 1864 (Miturgidae) and *Hibana velox* (Becker 1879) (Anyphaenidae), both highly active, quick-moving nocturnal foragers. Extrafloral nectar contributed significantly to survival and molting in prey-deprived *H. velox*. On a marginal diet of prey (one *Drosophila* adult on alternate days) offered to spiders as soon as they emerged, 97% of *C. mildei* underwent their first molt if they also received nectar, compared to 7% of controls without nectar. On a marginal diet of prey (one *Drosophila* adult on alternate days) offered to spiders starting two days after their emergence, 78% of the spiders also receiving nectar molted, compared to 0% of controls without nectar. Video recordings of activity showed that prey-deprived groups of *C. mildei* maintained their active nocturnal foraging for many days on nectar, whereas controls became increasingly quiescent until they died. Non-web-building spiders that feed on nectar may utilize its energy for foraging and thereby allocate the nutrients of prey to maintenance and growth.

Keywords: Diet, extrafloral, fitness, nutritional allocation, *Cheiracanthium mildei*, *Hibana velox*

As obligate carnivores, spiders are presumed to acquire their energy for maintenance, growth, and reproduction from captured prey. Attesting to their levels of activity (and resulting energetic needs), some wandering spiders encounter and eat insect eggs (Buschman et al. 1977; Nyffeler et al. 1990; Miliczky & Calkins 2002; Pfannenstiel 2004) and the eggs of other spiders (Willey & Adler 1989). As generalist predators, spiders are useful models for investigating invertebrate nutrient-specific selective foraging (Mayntz et al. 2005), but not all spiders should be presumed to be exclusively carnivorous or to get all of their energy from prey lipids. Coll & Guershon (2002) identify “true omnivory” (i.e., feeding on both plants and prey) in spiders, citing members of two families in particular: an araneid that feeds on pollen grains in the juvenile stage, which the spiderlings trap and eat incidentally when they eat and recycle their webs (Smith & Mommsen 1984), and an anyphaenid that feeds on plant nectar (Taylor & Foster 1996).

Compared to feeding on pollen grains, nectar feeding is a more directed behavior, which has been reported among all ages of spiders and among a number of different families. Independent observations of members of Thomisidae (crab spiders), Salticidae (jumping spiders), and the active, fast-moving Anyphaenidae, Miturgidae, and Corinnidae—all wanderers in foliage—suggest that all feed at the floral and extrafloral nectaries (EFNs) of plants (Edmunds 1978; Vogelei & Greissl 1989; Pollard et al. 1995; Ruhren & Handel 1999; Jackson et al. 2001). Applying what Singer & Bernays (2003) might call a “behavioral perspective,” Taylor & Pfannenstiel (2008) sampled spiders they deemed most likely to feed regularly on nectar from the EFNs of cotton plants and determined that one out of four were positive for ingested fructose, a plant-derived sugar. The survey also added members of Oxyopidae to the list of families that nectar feed. Considering that the hunting success rate for some wandering

spiders is thought to be low (Miyashita 1968; Anderson 1974; Nentwig 1987; Nyffeler et al. 1987; Nyffeler & Sterling 1994), we propose that plant sugars may be of direct benefit and help fuel the cursorial life of these spiders, allowing the valuable nutrients of prey to be allocated to the more complex metabolic processes of maintenance, growth, and reproduction.

Plant nectars contain primarily carbohydrates and water (Percival 1961), but also amino acids, lipids, vitamins, and minerals (Baker & Baker 1975, 1983; Koptur 1992). Nectar is exuded at floral nectaries, but unless a flower’s corolla is shallow, nectar is more accessible to spiders’ small mouthparts by way of extrafloral nectaries (EFNs), nectar-bearing tissues or structures that reside anywhere on a plant outside of a flower. EFNs often occur on leaves or leaf petioles, and take many forms, such as slits, cups, bowls, or undifferentiated tissue. Arthropods, particularly ants, often visit these open, accessible EFNs (Bentley 1977). Spiders observed at nectaries are non-web-building wanderers that inhabit vegetation, and their degree of activity and nectar feeding may be correlated. Searching for prey requires wandering, and frequent wandering means a greater likelihood of encountering EFNs and plant nectar. Plant nectar, which contains mostly sugar, could repay the energetic costs of wandering. The active foragers, *Cheiracanthium mildei* L. Koch 1864 (Miturgidae) and *Hibana velox* (Becker 1879) (Anyphaenidae), run throughout the vegetation at night, making them good candidates to investigate the energetic contributions of nectar. Both of these spiders have been observed at plant nectaries (Taylor & Foster 1996).

Three laboratory experiments tested the effects of extrafloral nectar on the survival, molting, and activity of newly emerged spiders. *Hibana velox* was the subject of initial survival tests. *Cheiracanthium mildei*, which is ecologically similar, was more easily obtained and the subject of later experiments. The experiments tested 1) the effects of nectar

and two concentrations of sucrose on the survival of individually housed *H. velox*, 2) the effect on molting in *C. mildei* by adding nectar to a marginal diet of prey (*Drosophila melanogaster*), and 3) the effects of nectar on the nocturnal running activity of small groups of prey-deprived *C. mildei*.

METHODS

Spiders.—Experimental *H. velox* were offspring of adults collected in 1994 in Alachua County, Gainesville, FL, USA; experimental *C. mildei* were offspring of adults collected in Franklin County, Columbus, Ohio, USA. Egg sacs were either collected in the field with adult females (which guard them) or produced by females maintained in the laboratory on a varied insect diet (mainly house flies and mosquitoes). Adults lived in 7-liter clear acrylic cages (15 × 21 × 27 cm) with a screened opening at one end and a sleeved opening at the other.

Experiments were conducted in a laboratory rearing room maintained on a 16:8 h light:dark diel cycle at ca 27° C and 80% relative humidity. Spiders were checked daily for molting and mortality. Each experiment or trial began within 12 h of spiderlings' emergence from their egg sacs, which was considered Day 0. "First molt," therefore, refers to a spider's first molt post-emergence.

Spiders were housed individually in clear, lidded, plastic containers, 5.2 cm diam. × 3.6 cm. Each container had four holes: two 12-mm, mesh-covered holes top and bottom; and two opposing 17-mm holes in the side wall, one mesh-covered and the other corked for introduction of prey and for changing the fluid wells of feeders. Feeders were small rectangles of plastic (1 × 2.5 cm) with a dimple (i.e., fluid well) drilled near each end (large dimple for water, small for nectar). Twenty of these small containers, composing an even mix of controls and treatment individuals, filled a large, clear, plastic 30 × 25 cm lidded box. Two boxes fit on a large plastic tray, lightly dusted with sifted sulfur to repel mites. Boxes were rotated daily.

Spiders in the activity trials were housed in small 7-cm-square plastic lidded boxes, each with four 17-mm holes, one on each side, three mesh-covered and one corked for introduction of spiders and for refilling fluid wells and changing feeders. Each box held four feeders, totaling eight fluid wells. For the control, all eight wells contained water; for the treatment, four wells contained water, and four contained nectar. Control and treatment boxes were placed side-by-side in a lidded clear plastic box, 35 × 24 cm and filmed with an RCA closed circuit TC7011 infrared-sensitive camera under continuous red light illumination, which does not disturb the spiders (Peck & Whitcomb 1970).

Diet.—In all experiments, water was available ad libitum. All containers that held spiders also held at least one feeder. In controls, both fluid wells of the feeder contained water. In treatment groups, the large well of the feeder contained water, and the small well contained either nectar or sucrose. Water also was available from soaked No.1 (9 mm) cotton dental balls. Ambient relative humidity was high, and smaller containers were kept in large boxes to keep water wells from drying out. The constant availability of free water ensured that spiders did not take nectar solely to obtain water. Sucrose and nectar, because of their viscosity, were delivered with a micro spatula in the smallest transferable amount, between 1–2 µl, smeared into the smaller fluid well of the plastic feeders.

Water, sucrose, and nectar were changed daily. Prey consisted of live, vestigial-winged *Drosophila melanogaster* maintained on instant (blue) *Drosophila* medium (Carolina Biological Supply). Diets combining prey and nectar were offered separately on alternate days to ensure that spiders were willing and able to consume nectar directly, rather than by way of prey that had ingested nectar.

All nectar was extrafloral to avoid introduction of pollen as a possible source of protein (Smith & Mommsen 1984). For the first trial of the first experiment with *H. velox*, extrafloral nectars were collected and combined from various greenhouse plants, such as *Hibiscus* and orchids. The nectar was slightly diluted to an unknown concentration to ease handling. For the second trial and all of the following experiments, nectar was undiluted and came solely from *Terminalia cattapa* (Indian almond, also growing in the university greenhouse), which produces copious nectar at EFNs on the base of the leaf near the petiole. Nectar from *T. cattapa* EFNs was 87.5% sugar constituents (variety unknown) determined from serial dilutions and a Reichert-Jung refractometer. The nectar was collected with a microspatula and stored at –45° C.

Experiments.—1. *Survival:* Two trials compared survival in individually housed *H. velox* on diets of water only, sucrose, or extrafloral plant nectar. For each trial, spiders from a single egg sac were divided among the control and two treatments. Both trials included a sucrose treatment to distinguish contributions of carbohydrates from possible contributions of other nectar components, such as amino acids or lipids. In the first trial, sucrose was relatively "low" (25%), in the second trial, "high" (69%), to more closely imitate the high sugar concentration of extrafloral nectars. Individuals were checked daily for mortality.

2. *Molting:* Two trials compared molting in individually housed *C. mildei* receiving marginal diets of prey (*Drosophila*) with and without nectar from *T. cattapa*. For each trial, spiders from a single egg sac were divided between the control and the treatment. In both trials, spiders were fed a single *Drosophila* adult on alternate days until the spider molted. On days without *Drosophila*, spiders received water (controls) or nectar. In the first trial, *Drosophila* were introduced on Day 1. In the second trial, introduction of *Drosophila* was delayed until Day 3. Nectar-fed spiders on the delayed *Drosophila* diet received nectar for the first two days. Spiders were part of the trial until they molted once.

3. *Activity:* Because both *H. velox* and *C. mildei* wander energetically in vegetation at night and are inactive during the day, we filmed two groups of cohabiting spiders at night in the laboratory, one with and one without access to nectar. Both had access to water ad libitum. For both replicates spiders from a single egg sac were divided between the control and treatment. From tapes, we quantified nightly activity as the number of spiders simultaneously running during a one-minute period at 10-min intervals, for 54 periods covering crepuscular light and the eight hours of scotophase. The mean of these 54 periods represented that night's activity.

Analysis: We analyzed data with *Statistica* for Windows (2000), StatSoft, Inc. Survival analysis (Kaplan-Meier) employed log-rank tests, which were adjusted for multiple comparisons, for which the calculated comparison-wise error rate of 0.008 is based on $K = 3$ treatments (Hardin et al. 1996).

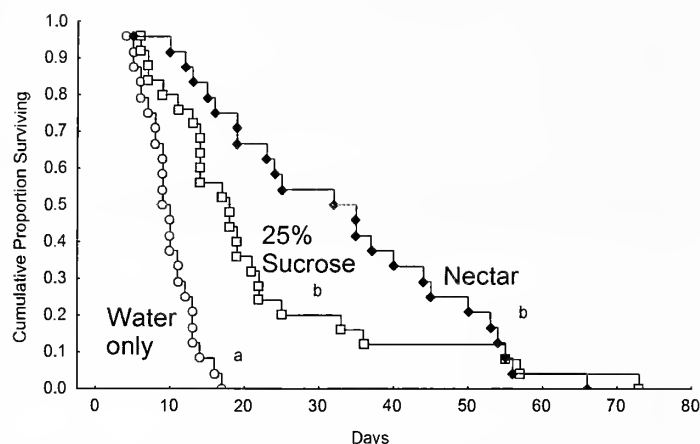


Figure 1.—Survival estimates for *Hibana velox* fed water only ($n = 24$), 25% sucrose ($n = 25$), or extrafloral nectar ($n = 24$). Curves with different letters are significantly different (adjusted pair-wise comparison).

We used chi-square tests to compare molting and the Mann-Whitney U -test to compare nocturnal activity.

RESULTS

1. Survival.—In the first trial, prey-deprived spiders survived significantly longer than water-only controls if they received 25% sucrose (log-rank test statistic = 3.71, $P = 0.0002$), or if they received nectar (log-rank test statistic = 4.39, $P = 0.0001$). The 25% sucrose and nectar treatments were not significantly different (log-rank test statistic = -1.43 , $P = 0.1566$) (Fig. 1). The second trial produced similar results. Spiders survived longer than water-only controls if they received 69% sucrose (log-rank test statistic = 3.36, $P = 0.0008$), or if they received nectar (log-rank test statistic = 3.66, $P = 0.0003$) (Fig. 2). The 69% sucrose and nectar treatments were not significantly different (log-rank test statistic = 0.770, $P = 0.4412$) (Fig. 2). Molting occurred in all of the groups except the controls of Trial 2 (Table 1).

2. Molting.—Both trials ended when all of the spiders in the nectarless control died, Day 15 for the first trial and Day 16 for the second. Nectar added to a marginal diet of prey (one *Drosophila* adult on alternate days) significantly increased the numbers of spiders that underwent their first molt whether the *Drosophila* diet began on Day 1 (97% vs. 7%) or Day 3 (78% vs. 0%). Delaying the introduction of prey, however, had a significant effect on the ability to survive the process of molting. Among the 97% (29/30) of spiders that molted receiving nectar and *Drosophila* on Day 1, 100% survived the molting process. Among spiders receiving nectar from Day 1 and *Drosophila* first on Day 3, 78% (38/49) initiated molting,

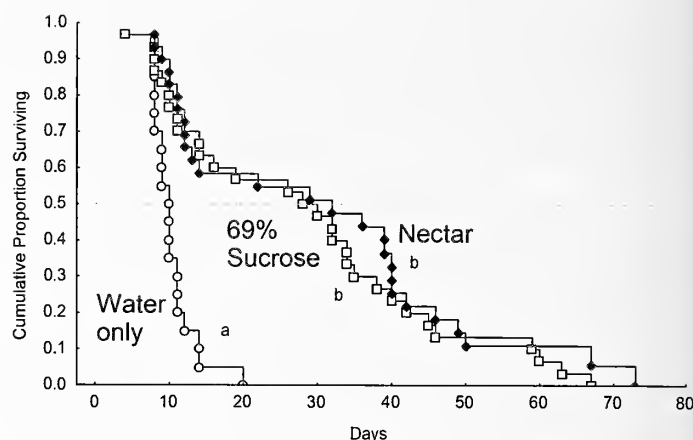


Figure 2.—Survival estimates of *Hibana velox* fed water only ($n = 20$), 69% sucrose ($n = 30$), or extrafloral nectar ($n = 30$). Curves with different letters are significantly different (adjusted pair-wise comparison).

but only 47% of the sample survived the molting process, a significant decrease in survival (multiple comparison χ^2 : prey on Day 1, $n = 30$; prey on Day 3, $n = 49$, $P < 0.001$).

Whether they received nectar or not, individual spiders on average consumed the same number of prey daily before an individual died or molted, calculated from the total number of *Drosophila* consumed in the experiment/total spider days survived. In the first trial, spiders with nectar ate 0.32 *Drosophila* daily and those without, 0.30 *Drosophila* (94 prey/294 d; 74 prey/243 d, respectively). In the second trial, spiders with nectar ate 0.26 *Drosophila* daily, and those without, 0.23 *Drosophila* (122 prey/466 d; 62 prey/265 d, respectively).

3. Activity.—The trials ended when any of the spiders died, which occurred in the nectarless control on Night 5 in the first replicate and on Night 4 in the second replicate. Comparisons of the total number of intervals of activity (270 for Replicate 1, 216 for Replicate 2) between the control and the nectar treatment show that nectar contributes significantly to the spider's running, in absence of prey (Mann-Whitney U : Replicate 1, $n = 270$ for both treatments, $Z = -12.709$, $P < 0.001$; Replicate 2, $n = 216$ for both treatments, $Z = -13.377$, $P < 0.001$). On Day 1, there was no significant difference in activity between spiders with and without nectar. On successive nights, spiders without nectar became increasingly quiescent until they died (Fig. 3). Individuals could not be distinguished from one another, and seven individuals at most could be distinguished running simultaneously, making the estimate of spider activity conservative.

Table 1.—Survival (mean \pm 1 SE) and molting of *Hibana velox* in two trials of survival on diets of water only, sucrose, or nectar. Significantly more spiders molted than their water-only controls if they received nectar or 69% sucrose (χ^2 , * $P < 0.05$, ** $P < 0.001$).

Trial	Diet	Survival (d)	Range (d)	1 st molt	n
1	Water only	9.8 \pm .7	4–17	17%	24
1	25% sucrose	22.0 \pm 3.4	6–73	28%	25
1	Nectar	32.6 \pm 3.6	5–66	50%*	24
2	Water only	10.4 \pm .7	8–20	0%	20
2	69% sucrose	28.4 \pm 3.4	4–67	63%**	30
2	Nectar	28.1 \pm 3.5	8–73	52%**	30

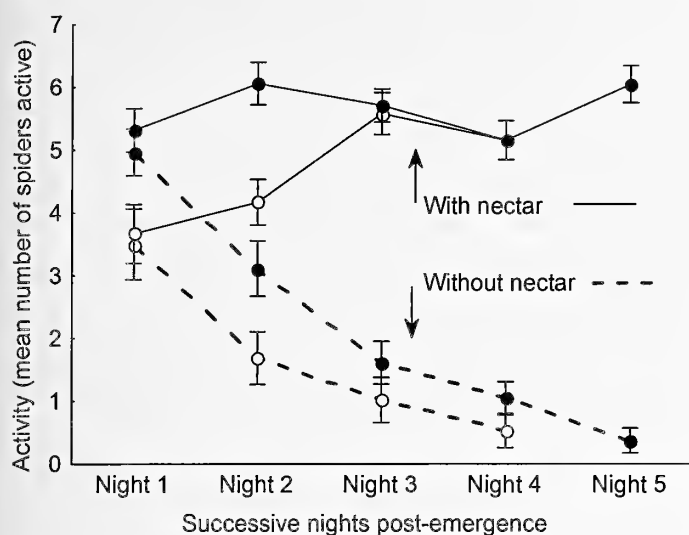


Figure 3.—Nocturnal activity of eight or nine cohabiting, newly emerged, prey-deprived *Cheiracanthium mildei*, with or without nectar. Replicate 1 (solid circles) without nectar, $n = 8$; with nectar, $n = 8$. Replicate 2 (open circles) without nectar, $n = 9$, with nectar, $n = 9$. "Activity" is the mean number of spiders simultaneously running during a one-minute period at 10-minute intervals for 54 periods. Points are means \pm SE.

DISCUSSION

In the lives of spiders, vegetation is considered important as a support for webs, as refugia, or as a food source for the insects that spiders catch (Turnbull 1973; Hatley & MacMahon 1980; Greenstone 1984; Uetz et al. 1999). Only recently have researchers considered the possibility of vegetation as a direct food source, and some spiders as true omnivores among terrestrial invertebrates. Taking this recognition one step further, we investigate why nectar feeding should be a likely activity among some spiders and for the first time measure the direct biological benefits to spiders that nectar-feed.

Why nectar feeding is a likely activity.—The likelihood that nectar can and does play a role in the energy budget of some spiders is unsurprising. Nectar's value as a dietary source of energy has been well established for nectarivorous insects, such as bees and butterflies; and predaceous arthropods other than spiders have been shown to survive periods of prey deprivation by feeding on plant nectars (Yokoyama 1978; Hagen 1987; van Rijn & Tanigoshi 1999; Limburg & Rosenheim 2001). Cursorial spiders that wander in vegetation with EFNs are likely to encounter nectar, which they have the potential to detect with "gustatory" hairs on their tarsi (Barth 2002). *Cheiracanthium mildei*, for example, oriented immediately to sugar and inserted its mouthparts as soon as a foretarsus touched it (RMT personal observation). Encountering nectar, spiders are predisposed to ingesting their food in liquid form, given their form of extra-oral digestion (Cohen 1998), which may also help them ingest nectars that can be too viscous for other nectar feeders to handle (Wäckers et al. 2001). Spiders respond positively to nectar, shown by preference tests (Jackson et al. 2001) and by their willingness to ingest chemicals, such as LSD, caffeine, and strychnine, if they are delivered in a sucrose solution (Christiansen et al. 1962; Witt 1971). And, both spiders that have been analyzed

for digestive enzymes (a tarantula and an agelenid) possess the enzyme sucrase (Pickford 1942; Mommsen 1977), which can digest nectar.

Concentration of sugars at EFNs.—Our experiments show that even when water was available, spiders still drank nectar when offered. *Hibana velox* without prey survived significantly longer and had a significantly higher incidence of molting than water-only controls if they had access to nectar or to the high (69%) concentration of sucrose (Table 1). Such high concentrations of sugar are not unusual in EFNs. The sugar concentration of *T. cattapa* extrafloral nectar that we determined to be 87.5% is nearly identical to the concentration of sugars (872 mg/ml) from the EFNs of castor bean (*Ricinus communis*) (Baker et al. 1978), and is similar to the concentration of sugar (77.7%) exuded at the EFNs of cashew (*Anacardium occidentale*) (Wunnachit et al. 1992). *Hibana velox* has been observed feeding at both of these species (Taylor & Foster 1996). Other *Hibana* spp. and *C. inclusum* have been observed at the EFNs of cotton (Taylor & Pfannenstiel 2008), which produce nectars with a sugar concentration between 62% (Wäckers et al. 2001) and 86% (Butler et al. 1972).

Nectar fulfills energy requirements.—In experiments providing *C. mildei* with *Drosophila* on Day 1, 97% of the spiders molted if they also had access to nectar, compared to 7% of controls without nectar. In experiments measuring activity, nectar contributed significantly to the energetic needs of *C. mildei*, conferring not only survival but also allowing them to keep up their frenetic running all night, every night that they were filmed. These results offer an opportunity to tease apart how these spiders are allocating nectar and prey-derived nutrients and can begin to address Uetz's (1992) question, "Is energy the sole currency involved in spider foraging, or do nutrients play a critical role?"

Both nectar and pure sucrose contributed to a higher incidence of molting in prey-deprived *H. velox* (Table 1), suggesting that it was the sugar component of nectar that contributed most to molting. Molting is an energy-depleting event that can increase respiration three-fold (Stranzy & Perry 1987). Nearly half of the components of a spider's cuticle, however, consist of proteins (Dalingwater 1987). Because sucrose contributed to the same incidence of molting as nectar, but molting requires not only carbohydrates but also protein for new cuticle, it appears that sugars fulfilled much of the energetic demand of sustained nocturnal locomotion (i.e., foraging), survival, and ecdysis (the molting event), allowing the protein contained in yolk reserves and prey to be allocated primarily to growth and/or new cuticle deposition. This may explain why *H. velox* provided with nectar but no prey survived long but did not grow (only some undergoing a single molt: Table 1), and why *C. mildei*—a larger spider at emergence with perhaps fewer reserves—provided with a marginal amount of prey but deprived of nectar, died early without molting. That is, a marginal amount of prey divided between activity and growth could not support both. The addition of nectar substantially changed the outcome: on average, both control and treatment *C. mildei* ingested nearly identical amounts of prey (0.30 vs. 0.32, and 0.23 vs. 0.26 *Drosophila*/spider/day in trials 1 and 2, respectively), but molted only if their diet was supplemented with nectar,

suggesting that they were at the margins of their nutritional requirements. Nectar feeding, by providing the energy for activity, may allow spiders to subsist on marginal amounts of prey, and, depending on the minimum amount required to reach functional maturity, might substantially reduce a spider's prey requirements. Spiders that can reduce their prey intake also are likely to reduce the energy and risk associated with attacking and subduing prey.

It is not clear why *C. mildei* receiving their initial *Drosophila* on Day 3 underwent a first post-emergent molt after consuming fewer prey than when *Drosophila* were introduced on Day 1. The consequences of delaying the introduction of prey by two days are dire: a 53% reduction in first-molt survival. This hints at some possible protein requirement for normal development within the first two days of spiderling emergence, or perhaps some developmental timeline triggered by the presence of protein in the diet. Fulfilling either of these requirements would make nectar-fueled survival and hunting all the more valuable.

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LITERATURE CITED

- Anderson, J.F. 1974. Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* (Hentz). *Ecology* 55:576–585.
- Baker, D.A., J.L. Hall & J.R. Thorpe. 1978. A study of the extrafloral nectaries of *Ricinus communis*. *New Phytologist* 81:129–137.
- Baker, H.G. & I. Baker. 1975. Studies of nectar constitution and pollinator-plant coevolution. Pp. 100–140. *In* *Coevolution of Animals and Plants*. (L.E. Gilbert & P.H. Raven, eds.). University of Texas Press, Austin, Texas.
- Baker, H.G. & I. Baker. 1983. A brief historical review of the chemistry of floral nectar. Pp. 126–152. *In* *The Biology of Nectaries*. (B. Bentley & T. Elias, eds.). Columbia University Press, New York.
- Barth, F.G. 2002. *A Spider's World: Senses and Behavior*. Springer, Berlin. 349 pp.
- Bentley, B.L. 1977. Extrafloral nectaries and protection by pugnacious bodyguards. *Annual Review of Ecology and Systematics* 8:407–427.
- Buschman, L.L., W.H. Whitcomb, R.C. Hemenway, D.L. Mays, R. Nguyen, N.C. Leppla & B.J. Smittle. 1977. Predators of velvetbean caterpillar eggs in Florida soybeans. *Environmental Entomology* 6:403–407.
- Butler, G.D., Jr, G.M. Loper, S.E. McGregor, J.L. Webster & H. Margolis. 1972. Amounts and kinds of sugar in the nectars of cotton (*Gossypium* spp.) and the time of their secretion. *Agronomy Journal* 64:364–368.
- Christiansen, A., R. Baum & P.N. Witt. 1962. Changes in spider webs brought about by mescaline, psilocybin, and increase in body weight. *Journal of Pharmacology and Experimental Therapeutics* 136:31–37.
- Cohen, A.C. 1998. Solid-to-liquid feeding: the inside(s) story of extraoral digestion in predaceous Arthropoda. *American Entomologist* 44:103–117.
- Coll, M. & M. Guershon. 2002. Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annual Review of Entomology* 47:267–297.
- Dalingwater, J.E. 1987. Chelicerate cuticle structure. Pp. 3–15. *In* *Ecophysiology of Spiders*. (W. Nentwig, ed.). Springer-Verlag, Berlin.
- Edmunds, M. 1978. On the association between *Myrmarachne* spp. (Salticidae) and ants. *Bulletin of British Arachnological Society* 4:149–160.
- Greenstone, M.H. 1984. Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. *Oecologia* 62:299–304.
- Hagen, K.S. 1987. Nutritional ecology of terrestrial insect predators. Pp. 533–577. *In* *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*. (F.J. Slansky & J.G. Rodriguez, eds.). John Wiley & Sons, New York.
- Hardin, M.J., J.L. Willers & T.L. Wagner. 1996. Nonparametric multiple comparisons of survivorship distributions. *Journal of Economic Entomology* 89:715–721.
- Hatley, C.L. & J.A. MacMahon. 1980. Spider community organization: seasonal variation and the role of vegetation architecture. *Environmental Entomology* 9:632–639.
- Jackson, R., S.D. Pollard, X.J. Nelson, G.B. Edwards & A.T. Barrion. 2001. Jumping spiders (Araneae: Salticidae) that feed on nectar. *Journal of Zoology (London)* 255:25–29.
- Koptur, S. 1992. Extrafloral nectar-mediated interactions between insects and plants. Pp. 81–129. *In* *Insect-Plant Interactions*. Volume IV. (E.A. Bernays, ed.). CRC Press, Boca Raton, Florida.
- Miliczky, E.R. & C.O. Calkins. 2002. Spiders (Araneae) as potential predators of leafroller larvae and egg masses (Lepidoptera: Tortricidae) in Central Washington apple and pear orchards. *Pan-Pacific Entomologist* 78:140–150.
- Limburg, D.D. & J.A. Rosenheim. 2001. Extrafloral nectar consumption and its influence on survival and development of an omnivorous predator, larval *Chrysoperla plorabunda* (Neuroptera: Chrysopidae). *Environmental Entomology* 30:595–604.
- Mayntz, D., D. Raubenheimer, M. Salomon, S. Toft & S.J. Simpson. 2005. Nutrient-specific foraging in invertebrate predators. *Science* 307:111–112.
- Miyashita, K. 1968. Growth and development of *Lycosa T-insignata* Boes. et Str. (Araneae: Lycosidae) under different feeding conditions. *Applied Entomology and Zoology* 3:81–88.
- Mommsen, T.P. 1977. Digestive enzymes of a spider (*Tegenaria arctica* Koch). II. Carbohydrases. *Comparative Biochemistry and Physiology* 60A:371–375.
- Nentwig, W. 1987. The prey of spiders. Pp. 249–263. *In* *Ecophysiology of spiders*. (W. Nentwig, ed.). Springer, Berlin.
- Nyffeler, M., R.G. Breene, D.A. Dean & W.L. Sterling. 1990. Spiders as predators of arthropod eggs. *Journal of Applied Entomology* 109:490–501.
- Nyffeler, M., D.A. Dean & W.L. Sterling. 1987. Predation by green lynx spider, *Peucetia viridans* (Araneae: Oxyopidae), inhabiting cotton and woolly croton plants in East Texas. *Environmental Entomology* 16:356–359.
- Nyffeler, M. & W.L. Sterling. 1994. Comparison of the feeding niche of polyphagous insectivores (Araneae) in a Texas cotton plantation: estimates of niche breadth and overlap. *Environmental Entomology* 23:1294–1303.
- Peck, W.B. & W.H. Whitcomb. 1970. Studies on the biology of a spider, *Chiracanthium inclusum* (Hentz). University of Arkansas, Agricultural Experiment Station Bulletin 753. 76 pp.
- Percival, M.S. 1961. Types of nectar in angiosperms. *New Phytologist* 60:235–281.
- Pfannenstiel, R.S. 2004. Nocturnal predation of lepidopteran eggs in south Texas cotton—2002. Pp. 1594–1600. *In* *Proceedings of the*

- Beltwide Cotton Conference. National Cotton Council, Memphis, Tennessee.
- Pickford, G.E. 1942. Studies on the digestive enzymes of spiders. Transactions of the Connecticut Academy of Arts and Sciences 35:33–72.
- Pollard, S.D., M.W. Beck & G.N. Dodson. 1995. Why do male crab spiders drink nectar? Animal Behaviour 49:1443–1448.
- Ruhren, S. & S.N. Handel. 1999. Jumping spiders (Salticidae) enhance the seed production of a plant with extrafloral nectaries. Oecologia 119:227–230.
- Singer, M.S. & E.A. Bernays. 2003. Understanding omnivory needs a behavioral perspective. Ecology 84:2532–2537.
- Smith, R.B. & T.P. Mommsen. 1984. Pollen feeding in an orb-weaving spider. Science 226:1330–1333.
- Stranzy, F. & S.F. Perry. 1987. Respiratory system: structure and function. Pp. 78–94. In Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.
- Taylor, R.M. & W.A. Foster. 1996. Spider nectarivory. American Entomologist 42:82–86.
- Taylor, R.M. & R.S. Pfannenstiel. 2008. Nectar feeding by wandering spiders on cotton plants. Environmental Entomology 37:996–1002.
- Turnbull, A.L. 1973. Ecology of the true spiders (Araneomorphae). Annual Review of Entomology 18:305–348.
- Uetz, G.W. 1992. Foraging strategies of spiders. Trends in Ecology & Evolution 7:155–158.
- Uetz, G.W., J. Halaj & A.B. Cady. 1999. Guild structure of spiders in major crops. Journal of Arachnology 27:270–280.
- van Rijn, P.C.J. & L.K. Tanigoshi. 1999. The contribution of extrafloral nectar to survival and reproduction of the predatory mite *Iphiseius degenerans* on *Ricinus communis*. Experimental & Applied Acarology 23:281–296.
- Vogelei, A. & R. Greissl. 1989. Survival strategies of the crab spider *Thomisus onustus* Walckenaer 1806 (Chelicerata, Arachnida, Thomisidae). Oecologia 80:513–515.
- Wäckers, F.L., D. Zuber, R. Wunderlin & F. Keller. 2001. The effect of herbivory on temporal and spatial dynamics of foliar nectar production in cotton and castor. Annals of Botany 87:365–370.
- Willey, M.B. & P.H. Adler. 1989. Biology of *Psecutia viridans* (Araneae, Oxyopidae) in South Carolina, with special reference to predation and maternal care. Journal of Arachnology 17:275–284.
- Witt, P.N. 1971. Drugs alter web-building of spiders. A review and evaluation. Behavioral Science 16:98–113.
- Wunnachit, W.C., C.F. Jenner & M. Sedgley. 1992. Floral and extrafloral nectar production in *Anacardium occidentale* L. (Anacardiaceae): an andromonoecious species. International Journal of Plant Science 153:413–420.
- Yokoyama, V.Y. 1978. Relation of seasonal changes in extrafloral nectar and foliar protein and arthropod populations in cotton. Environmental Entomology 7:799–802.

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SHORT COMMUNICATION

Caddo agilis and *C. pepperella* (Opiliones, Caddidae) diverged phylogenetically before acquiring their disjunct, sympatric distributions in Japan and North America

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Abstract. The harvestmen *Caddo agilis* Banks 1892 and *C. pepperella* Shear 1975 (Caddidae, Caddinae) share a disjunct distribution in eastern Asia and eastern North America that has been attributed to either recent (Pleistocene) evolution of a *C. pepperella* morph from *C. agilis* in each region or to a pre-glacial separation within each of two established species. The present study used 2,130-base sequences from two nuclear protein-coding genes (EF1 α , Pol II) to test the phylogenetic predictions of both hypotheses using representatives from the two *Caddo* species from both regions and two acropsopilionine outgroup species. The results supported the hypothesis that the two *Caddo* species were distinct prior to their respective biogeographic disjunctions; *C. agilis* and *C. pepperella* were each recovered as monophyletic and each appears to have undergone separation into Asian and North American groups.

Keywords: Harvestmen, phylogeny, elongation factor-1 α , RNA polymerase II

This study focuses on the phylogeny and biogeography of the two extant species of *Caddo*, *C. agilis* Banks 1892 and *C. pepperella* Shear 1975 (Caddidae, Caddinae), both of which occur in eastern North America and Japan. Two scenarios have been offered in the arachnological literature to explain the disjunct sympatric distribution of the two species: the parallel-evolution hypothesis (Shear 1975, 1996, 2004) and the habitat-fragmentation hypothesis (Suzuki 1976). Shear (1975) originally suggested that the smaller *C. pepperella* evolved in North America as a paedomorphic (progenetic) variant of *C. agilis*, perhaps as an adaptation to shorter growing seasons associated with glacial conditions during the Pleistocene. The subsequent discovery of *C. pepperella* in Japan (Suzuki 1976) was inconsistent with Shear's hypothesis, as it seemed to require an improbable recent dispersal between eastern North America and Japan. Shear (1996, 2004) countered that a *C. pepperella* morph may have evolved independently in North America and Japan during the Pleistocene. In contrast, Suzuki (1976) proposed that both species originally inhabited an ancient circumboreal ecosystem that now consists of isolated postglacial fragments in eastern Asia and eastern North America.

The parallel-evolution and habitat-fragmentation hypotheses can be tested by means of molecule-based phylogenetic analysis, with the former predicting diphyley within *C. pepperella* and the latter predicting monophyly of both *C. agilis* and *C. pepperella* across their ranges. Here we test these hypotheses using 2,130 base pairs of the nuclear protein-coding genes elongation factor-1 α (EF-1 α) and RNA polymerase II (Pol II) from representative *C. agilis* and *C. pepperella* from North America and Japan as well as two acropsopilionine outgroup species, *Austropsopilio sudamericus* Shultz & Cekalovic 2003 and *Acropsopilio chilensis* Silvestri 1904. Our results corroborate Suzuki's habitat-fragmentation hypothesis.

METHODS

Terminal taxa and sequences.—Specimens were collected alive and preserved in > 95% ethanol. They were stored in > 95% ethanol at –20° C up to 2 yr prior to RNA extraction. The analysis was based on sequences from six specimens, with collection data and GenBank accession numbers as follows:

1. *Caddo agilis* Banks 1892. USA: *New Hampshire*: Cheshire County, Pisgah State Park, 42.868°N, 72.448°W, 7–11 July 2001, J.W. Shultz (EF-1 α : FJ361272; Pol II: FJ476262–FJ476264).
2. *Caddo agilis* Banks 1892. JAPAN: *Tottori Prefecture*: Chizurho, Ashizu Tunnel, 660 m, 20 June 1998, N. Tsurusaki (EF-1 α : AF240838; Pol II: AH010430).
3. *Caddo pepperella* Shear 1975. USA: *New Hampshire*: Cheshire County, Pisgah State Park, 42.868°N, 72.448°W, 7–11 July 2001, J.W. Shultz (EF-1 α : FJ361272; Pol II: FJ476265–FJ476267).
4. *Caddo pepperella*. JAPAN: *Tottori Prefecture*: Mt. Nagi, 630 m elev., 20 June 1998, N. Tsurusaki (EF-1 α : AF240863; Pol II: AH010457).
5. *Acropsopilio chilensis*. CHILE: *Provincia de Concepcion*: Cerro Caracol, 5 October 2003, T. Cekalovic (EF-1 α : FJ361275; Pol II: FJ476256–FJ476258).
6. *Austropsopilio sudamericus*. CHILE: *Provincia de Valdivia*: Cerro Oncol, April 2001, T. Cekalovic (EF-1 α : FJ361274; Pol II: FJ476259–FJ476261).

A voucher specimen of each species is deposited in the National Museum of Natural History (Smithsonian Institution) except for *C. pepperella* from Japan, because the only specimen available was consumed in genomic extraction.

Molecular methods.—Detailed procedures for generating sequence data, including primer sequences, have been published elsewhere (Regier & Shultz 1997). In brief, total nucleic acids were isolated; complementary DNA of EF-1 α and Pol II mRNA was made by reverse transcription; ds-DNA copies were amplified by PCR and subsequently gel isolated; the resulting PCR fragments were used as templates for another round of PCR amplification with nested primers; and the resulting fragments were gel isolated and sequenced. When the resulting fragment concentration was too low to sequence directly, it was either concentrated or reamplified using the M13 sequences present at the 5' ends of all primers. The same M13

sequences were also used as primers for thermal cycle/dideoxy sequencing. Sequencing reactions were fractionated and preliminary analyses were performed with Perkin-Elmer/ABI automated DNA sequencers. Automated DNA sequencer chromatograms were edited and contigs were assembled using the pregap and gap4 programs within the Staden software package (Staden et al. 1999). Sequences were aligned and Nexus-formatted nucleotide data sets were constructed using the Genetic Data Environment, version 2.2 (Smith et al. 1994). All sequences lacked indels. Amino acid data were inferred from nucleotide sequences using the universal nuclear genetic code option in MacClade, ver. 3.08 (Maddison & Maddison 1992).

Phylogenetic analysis.—Parsimony analyses of three data sets [all nucleotides (*ntl-3*), third codon positions (*nt3*) and inferred amino acids (*aa*)] were performed in PAUP4.0 (Swofford 1998) using unordered, equally weighted characters. Analyses consisted of exhaustive searches followed by bootstrap analyses (Felsenstein 1985) based on branch-and-bound searches of 1,000 pseudoreplicates. In conducting maximum-likelihood (ML) analysis, the program Modeltest, ver. 3.7 (Posada & Crandall 1998) was used to choose a model for the *ntl-3* and *nt3* data sets using AIC (Posada & Buckley 2004), with specific parameter values being estimated during subsequent phylogenetic analysis. The ML analyses were conducted in PAUP* using exhaustive searches and nonparametric bootstrap analyses were performed using branch-and-bound searches of 1,000 pseudoreplicates.

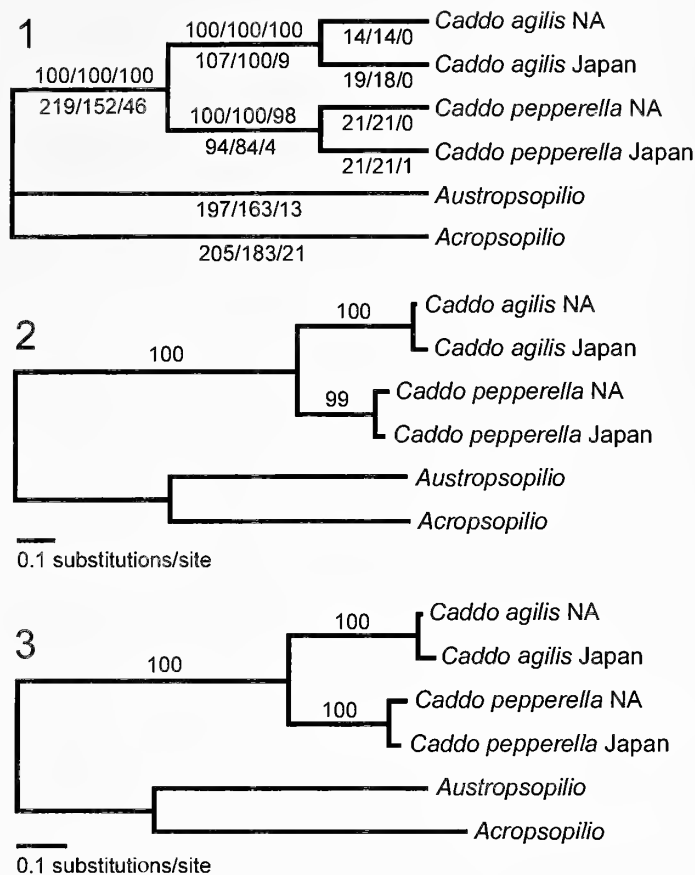
RESULTS

Parsimony analyses of all nucleotides (*ntl-3*), 3rd codon positions (*nt3*) and inferred amino acids (*aa*) produced identical, fully resolved topologies with bootstrap percentages (BP) of 98–100 for all internal nodes (Fig. 1) (*ntl-3*: 2,130 characters, 398 informative, length = 897, CI = 0.8305; *nt3*: 710 characters, 317 informative; length = 756, CI = 0.816; *aa*: 710 characters, 55 informative; length = 94, CI = 0.9492). *Caddo agilis* and *C. pepperella* were each recovered as monophyletic and reconstructed as sister groups with respect to the acropsopiliines, *Acropsopilio chilensis* and *Austropsopilio sudamericanus*.

Comparison of alternative likelihood models in Modeltest indicated that the *ntl-3* data should be analyzed using a GTR+ Γ_4 +I model and that the *nt3* matrix should be analyzed under the TVM+ Γ_4 model. Exhaustive likelihood searches using these models recovered topologies identical to those derived from parsimony-based analyses (*ntl-3*: -ln likelihood = 6649.2923; *nt3*, -ln likelihood = 3391.9731). Specifically, the clades *C. agilis*, *C. pepperella*, and *Caddo* were each recovered as monophyletic with strong support (BP 99–100%) (Figs. 2, 3), a result predicted by Suzuki's hypothesis. The two data sets were reanalyzed under their respective models with the analyses constrained to yield Shear's hypothesis of independent evolution of *C. pepperella* from *C. agilis* in Asia and North America and Suzuki's hypothesis of monophyly of both *C. agilis* and *C. pepperella* throughout their ranges. Kishino-Hasegawa tests (Kishino & Hasegawa 1989) showed the trees constrained to the prediction of Shear's hypothesis to be significantly less likely than those constrained to Suzuki's hypothesis ($P < 0.001$).

DISCUSSION

Our results indicate that *Caddo agilis* and *Caddo pepperella* are monophyletic species that diverged phylogenetically before each acquired a disjunct geographic distribution in Japan and eastern North America. This supports Suzuki's (1976) habitat-fragmentation hypothesis and is inconsistent with Shear's (1975, 1996, 2004) parallel-evolution hypothesis. These findings are consistent with current understanding of climatic and biogeographic events during the late Tertiary (Sanmartín et al. 2001). The eastern Asia-eastern North America disjunction exemplified by *Caddo* parallels a long-known biogeographic pattern among flowering plants (Wen 1999; Xiang et al. 2000). During the mid-Cenozoic, eastern Asia and eastern North



Figures 1–3.—Results of phylogenetic analysis. 1. Parsimony tree based on separate analysis of all nucleotides, third codon positions and inferred amino acids, respectively. Numbers above branches are non-parametric bootstrap percentages based on 1000 pseudoreplicates. Numbers below branches are estimated branch lengths under acctran optimization. 2. Maximum-likelihood tree based on all nucleotides using the GTR + Γ_4 + I model. 3. Maximum-likelihood tree based on third codon positions using the TVM + Γ_4 model.

America were spanned by mesophytic forests that were eventually separated into Asian and American components during the early Pliocene, a culmination of long-term trends in the cooling and drying of central and northern North America. As a consequence, many plant genera have representative species in both eastern Asia and eastern North America, and relative rates tests conducted on 12 species pairs using the *rbcL* gene indicated a divergence time of 5.4 ± 2.6 million years ago (Xiang et al. 2000). Zoologists have not explored the Asian-North American disjunction to the same extent as botanists, but several examples are known among animals (Sanmartín et al. 2001), including the non-caddine harvestmen *Acropsopilio hoopis* (Crosby 1904) and *Crosbycus dasyncnemus* (Crosby 1911), *Okeantobates* millipedes (Engel 1993), plethodontid salamanders (Min et al. 2005) and, among late Tertiary fossils, lesser pandas and meline badgers (Tedford & Harington 2003; Wallace & Wang 2004).

In contrast, because the two *Caddo* species are roughly sympatric and often syntopic in both North America and Japan, vicariant or climatic events cannot readily explain their phylogenetic divergence or morphological differences. It is possible that the two extant *Caddo* species diverged due to resource or habitat partitioning, as *C. agilis* tends to occupy exposed surfaces (e.g., tree trunks, logs, stones) and *C. pepperella* occurs on the ground in the leaf litter and under fallen objects (Suzuki 1976; Shultz, unpubl. obs.). Given the similarity between *C. pepperella* and juvenile *C. agilis*, it is possible that such habitat specialization produced morphological differences between the

two species via heterochrony, in a manner similar to that proposed by Shear (1975, 1996, 2004). Still, there is no clear evidence as to whether *C. agilis* is peramorphic with respect to its ancestor, whether *C. pepperella* is pedomorphic with respect to its ancestor, both, or neither. Outgroup comparison with the small soil- or litter-dwelling acropsopilionines (Caddidae) would seem to favor *C. pepperella* as the better model for the common ancestor of extant *Caddo* and thus evolution of *C. agilis* via hypermorphosis. However, without relevant information about the morphology and development of ancestral and extant *Caddo*, this matter will remain an exercise in speculation.

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LITERATURE CITED

- Enghoff, H. 1993. Phylogenetic biogeography of a Holarctic group: the julidan millipedes. Cladistic subordinateness as an indicator of dispersal. *Journal of Biogeography* 20:525–536.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39:783–791.
- Kishino, H. & M. Hasegawa. 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea. *Journal of Molecular Evolution* 29:170–179.
- Maddison, W.P. & D.R. Maddison. 1992. *MacClade: Analysis of Phylogeny and Character Evolution*. Version 3. Sinauer Associates, Sunderland, Massachusetts. 398 pp.
- Min, M.S., S.Y. Yang, R.M. Bonett, D.R. Vieites, R.A. Brandon & D.B. Wake. 2005. Discovery of the first Asian plethodontid salamander. *Nature* 435:87–90.
- Posada, D. & T.R. Buckley. 2004. Model selection and model averaging in phylogenetics: advantages of Akaike Information Criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology* 53:793–808.
- Posada, D. & K.A. Crandall. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:917–918.
- Regier, J.C. & J.W. Shultz. 1997. Molecular phylogeny of the major arthropod groups indicates polyphyly of crustaceans and a new hypothesis for the origin of hexapods. *Molecular Biology and Evolution* 14:902–913.
- Sanmartín, I., H. Enghoff & F. Ronquist. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society* 73:345–390.
- Shear, W.A. 1975. The opilionid family Caddidae in North America, with notes on species from other regions (Opiliones, Palpatores, Caddoidea). *Journal of Arachnology* 2:65–88.
- Shear, W.A. 1996. *Hesperopilio mainae*, a new genus and species of harvestman from Western Australia (Opiliones: Caddidae: Acropsopilioninae). *Records of the Western Australian Museum* 17:455–460.
- Shear, W.A. 2004. Description of the female of *Acropsopilio chomulae* (Goodnight & Goodnight 1948) from Chiapas, Mexico (Opiliones, Caddidae, Acropsopilioninae). *Journal of Arachnology* 32:432–435.
- Smith, S.W., R. Overbeek, C.R. Woese, W. Gilbert & P.M. Gillevet. 1994. The genetic data environment and expandable GUI for multiple sequence analysis. *Computer Applications in the Biosciences* 10:671–675.
- Staden, R., K.F. Beal & J.K. Bonfield. 1999. The Staden Package, 1998. Pp. 115–130. *In* *Bioinformatics Methods and Protocols*. (S. Misener & S. Krawetz, eds.). The Humana Press, Totowa, New Jersey.
- Suzuki, S. 1976. The harvestmen of the family Caddidae in Japan (Opiliones, Palpatores, Caddoidea). *Journal of Science, Hiroshima University, Series B, Division 1* 26:261–273.
- Swofford, D.L. 1998. PAUP* 4.0 Beta Version. Sinauer Associates: Sunderland, Massachusetts.
- Tedford, R.H. & C.R. Harington. 2003. An arctic mammal fauna from the early Pliocene of North America. *Nature* 425:388–390.
- Wallace, S.C. & X. Wang. 2004. Two new carnivores from an unusual late Tertiary forest biota in eastern North America. *Nature* 431:556–559.
- Wen, J. 1999. Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants. *Annual Review of Ecology and Systematics* 30:421–455.
- Xiang, Q.-Y., D.E. Soltis, P.S. Soltis, S.R. Manchester & D.J. Crawford. 2000. Timing of the eastern Asian-eastern North American floristic disjunction: molecular clock corroborates paleontological estimates. *Molecular Phylogenetics and Evolution* 15:462–472.

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SHORT COMMUNICATION

New spider host associations for three acrocerid fly species (Diptera, Acroceridae)

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Abstract. Acrocerid flies are endoparasitoids of spiders. New host associations are reported for *Ogcodes melampus* Loew 1872, *O. eugonatus* Loew 1872, and *Acrocera* sp. (Group IV; *sensu* Sabrosky 1944) from reared individuals of two Salticidae species, *Pelegrina proterva* (Walckenaer 1837) (both *Ogcodes* species), and *Eris militaris* (Hentz 1845) (the *Acrocera* sp.) (Group IV; *sensu* Sabrosky 1944). The spiders were sampled in the canopy and understorey of a mature north-temperate hardwood forest at the Morgan Arboretum, Québec, Canada.

Keywords: Endoparasitoids, Salticidae, canopy, maple, beech

Acrocerid flies (Diptera, Brachycera) are endoparasitoids of spiders. Each larval instar is morphologically unique and has a distinctive lifestyle (hypermetamorphosis: Schlinger 1987). Their planidial first instar larvae actively seek their spider host or, only in the genus *Acrocera*, attach themselves to the substrate where they have hatched, waiting for a host spider to pass by (Schlinger 1987, 2003; Nielsen et al. 1999). Once a host is found, the planidium climbs on to the spider, migrates to the spider's abdomen, and cuts a small hole to enter the spider en route to the booklungs (Schlinger 1987; see Nielsen et al. 1999, for an alternative strategy to enter the host). In the booklungs, the larva molts again, attaches itself to a booklung, and enters a resting stage. After molting, the fourth instar larva feeds actively inside the spider and causes the parasitized spider to spin a molting-web like retreat. The acrocerid larva then emerges from the spider, finishes feeding, fixes itself to the web and pupates (Schlinger 1987). Acrocerid flies show a preference for wandering, fossorial, and web-building spiders that live close to the ground and wander in adjacent vegetation (Cady et al. 1993).

We report new spider (Araneae) host associations for *Ogcodes melampus* Loew 1872, *O. eugonatus* Loew 1872, and *Acrocera* sp. (Group IV; *sensu* Sabrosky 1944) (Diptera: Acroceridae). Foliage spiders were sampled by beating live and dead branches between 10 May and 24 September 2007 in the canopy of mature trees and understorey saplings of sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Eher.) at the Morgan Arboretum, Sainte-Anne-de-Bellevue, Québec, Canada (45°25'55"N; 73°56'58"W). In the laboratory, the spiders were housed individually in small plastic containers and kept alive in preparation for a ballooning dispersal experiment.

During this experiment, cream yellow pupae were noticed inside containers of three, dead, sub-adult individuals of *Pelegrina proterva* (Walckenaer 1837) (Araneae: Salticidae, body size = 3.9 mm, $n = 4$). Two of these individuals of *P. proterva* were sampled in the canopy of mature American beech trees and one in the canopy of a mature sugar maple on 7 June 2007. Adult flies emerged in the plastic containers approximately 28 days later, in early July 2007. The adults were determined to be two females of *O. eugonatus* (one from American beech and the other from sugar maple) and one female of *O. melampus* (from American beech).

In similar fashion, a female *Acrocera* sp. (Group IV, near female 1 *sensu* Sabrosky 1948) emerged from a sub adult individual of *Eris militaris* (Hentz 1845) (Araneae: Salticidae, body size = 5.2 mm, $n = 6$). This individual of *E. militaris* was sampled on an American beech sapling in the understorey on 3 July 2007, the acrocerid larva had pupated a week later, and the adult fly emerged approximately 2 wk

later. Overall, 0.88 percent of the spiders in our study were parasitized by Acroceridae.

Acrocera is known to lay its eggs on grass stems (Schlinger 1987), potentially not far removed from American beech saplings. *Eris militaris*, the host spider, is also significantly associated with the understorey layer in this habitat type (Larrivée & Buddle 2008). In contrast, the three infected individuals of *P. proterva* originated from the canopy. Females from the genus *Ogcodes* lay their eggs on the tips of dead twigs (Schlinger 1987), common in the canopy of beech trees. Only four acrocerid parasites were found in our study but the rarity of these flies makes this an important life history observation. *Ogcodes* specimens were only in spiders from the canopy and the *Acrocera* specimen in an understorey spider. Future research on hardwood forest *Ogcodes* and *Acrocera* species should test their potential preference for canopy and understorey spiders respectively.

Ogcodes melampus is mainly found in the western part of North America with previous records placing it as far east as Minnesota (Schlinger 1960). This specimen represents a significant range extension for this species. Other northeastern specimens of *O. melampus* were found in the Canadian National Collection in Ottawa, from both Michigan and Ontario. There is no life history available for this species (Schlinger 1960) and it has been reared from only two spider species, a lycosid and a thomisid (Schlinger 1987). Our record adds the family Salticidae and the species *P. proterva* to its host list. *Ogcodes eugonatus* has been reared from Lycosidae, Oxyopidae, Thomisidae, and Salticidae (species are listed in Schlinger 1987) though this is the first record of this species from a *P. proterva* host.

The genus *Acrocera* occurs across North America though records from *Acrocera* Group IV (*sensu* Sabrosky 1944) mostly originate from eastern North America. They are known endoparasitoids of seven spider families: Plectreuridae, Lycosidae, Agelenidae, Amaurobiidae, Clubionidae, Gnaphosidae, and Salticidae (Schlinger 1987). *Acrocera bulla* Westwood, a member of Group IV, is the only other known species from the genus *Acrocera* that is an endoparasitoid of the family Salticidae. Our observation adds *E. militaris* to the host list of spiders for the genus *Acrocera*.

Specimens are deposited at the Lyman Entomological Museum, McGill University, Macdonald Campus, Ste-Anne-de-Bellevue, Québec, Canada.

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Morgan Arboretum. Jeff Cumming from the Diptera section at the Canadian National Collection kindly provided determined specimens of *Ogcodes* and *Acrocera* for comparison. Finally, we thank Robb Bennett and two anonymous reviewers for comments on an early draft of the manuscript.

LITERATURE CITED

- Cady, A., R. Leech, L. Sorkin, G. Stratton & M. Caldwell. 1993. Acrocerid (Insecta: Diptera) life histories, behaviours, host spiders (Arachnida: Araneida), and distribution records. *Canadian Entomologist* 125:931–944.
- Larri  e, M. & C.M. Buddle. 2008. Diversity of canopy and understorey spiders in north-temperate hardwood forests. *Agricultural and Forest Entomology*. DOI: 10.1111/j.1461-9563.2008.00421.x
- Nielsen, B.O., P. Funch & S. Toft. 1999. Self-injection of a dipteran parasitoid into a spider. *Naturwissenschaften* 86:530–532.
- Sabrosky, C.W. 1944. A revision of the American spider parasites of the genera *Ogcodes* and *Acrocera* (Diptera, Acroceridae). *American Midland Naturalist* 31:385–413.
- Sabrosky, C.W. 1948. A further contribution to the classification of the North American spider parasites of the family Acroceridae (Diptera). *American Midland Naturalist* 39:382–430.
- Schlinger, E.I. 1960. A revision of the genus *Ogcodes* Latreille with particular reference to species of the western hemisphere. *Proceedings of the United States National Museum* 111:227–336.
- Schlinger, E.I. 1987. The biology of Acroceridae (Diptera): true endoparasitoids of spiders. Pp. 319–327. *In* *Ecophysiology of Spiders*. (W. Nentwig, ed.). Springer-Verlag, Berlin.
- Schlinger, E.I. 2003. Acroceridae, spider-fly endoparasitoids. Pp. 734–740. *In* *The Natural History of Madagascar*. (S.M. Goodman & J.P. Benstead, eds.). University of Chicago Press, Chicago.

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SHORT COMMUNICATION

Description of *Toca*, a new neotropical spider genus (Araneae, Ctenidae, Caloeteninae)

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Abstract. *Toca* new genus is proposed to include two new species: the type species *T. bossanova* new species from Rio de Janeiro, Brazil, and *T. samba* new species from Paraná and Minas Gerais, Brazil. *Toca* may be related to *Caloctenus* Keyserling and *Gephyroctenus* Mello-Leitão, with which it shares the scales on the abdominal dorsum and the epigynum as a single, slightly sclerotized, fold. The genus can be distinguished among the Caloeteninae genera by its unique genital structures.

Keywords: Systematics, taxonomy, Brazil

The subfamily Caloeteninae was proposed by Simon (1897) based mainly on the shape of the labium, sternum, and carapace; and by the numerous and elongated spines on the first and second pairs of legs. Currently it contains four genera: *Caloctenus* Keyserling 1877 and *Gephyroctenus* Mello-Leitão 1936, both from South America; *Diallomus* Simon 1897 from Sri Lanka; and *Apolania* Simon 1898 from the Seychelles Islands (Silva 2003; Platnick 2008). The subfamily is characterized by the following synapomorphies: presence of a set of elongated spines on tibia and metatarsus of the first and second pairs of legs, six thickened and elongated setae on the anal tubercle, and a reduced number of cylindrical gland spigots on the posterior median spinnerets (Silva 2003).

In addition to the four Caloeteninae genera already described, we propose the new genus *Toca* to include two new species: *T. bossanova* from Rio de Janeiro, Brazil, and *T. samba* from Paraná and Minas Gerais, Brazil. *Toca* may be related to *Caloctenus* and *Gephyroctenus*, with which it shares scales on the abdominal dorsum and epigynum as a single, slightly sclerotized fold (Silva 2003, 2004; Polotow & Brescovit 2008). *Toca* can be distinguished by the unique genital structures within the subfamily, which support the proposal of a new genus. The material examined belongs to Instituto Butantan, São Paulo (IBSP, A. D. Brescovit) and Muséum National d'Histoire Naturelle, Paris (MNHN, C. Rollard). All measurements are in millimeters. Terminology follows Silva (2003).

TAXONOMY

Ctenidae Keyserling 1877

Caloeteninae Simon 1897

Toca new genus

Figs. 1–9

Type species.—*Toca bossanova* new species

Etymology.—The generic name is an arbitrary combination of letters. The gender is feminine.

Diagnosis.—*Toca* resembles *Caloctenus* and *Gephyroctenus* by the presence of scales on the abdominal dorsum (Silva 2003; Silva 2004). Males can be distinguished by an embolus with a rounded base (Figs. 4, 8) and large conductor (Figs. 1, 7) with a surrounding groove to accommodate the embolus (Figs. 3, 8). The female of *T. bossanova* resembles the female of *Diallomus fuliginosus* (type

specimen, deposited in MNHN, examined) with the epigynum containing a slightly sclerotized single fold and an anterior hood (Fig. 5). The female can be distinguished from the remaining genera by the elongated copulatory ducts and anterior glandular projection (Fig. 6) of the epigynum. The female of *T. samba* is unknown.

Description.—Ecribellate ctenids. Total body length (males and females) 3.40–4.40. Carapace pale brown with longitudinal lighter stripe from eyes to posterior margin of carapace; chelicerae, labium, endites, sternum, and legs pale brown; posterior median and lateral eyes on black tubercles; legs with dorsal, transverse dark spots. Carapace flattened. Eyes: ctenoid pattern, 2–4–2. Chelicerae: three prolateral teeth and five to six small retrolateral teeth. Labium short, wider than long. Fovea short, positioned in posterior third of carapace. Legs I and II with set of numerous elongated spines on femur, tibia, and metatarsus. Trochanter slightly notched. Abdomen flattened, subpentagonal. Six erect bristles distally positioned on anal tubercle. Palp: tibia short; RTA divided into ventral and dorsal branches (Figs. 1, 2, 7, 9); cymbium with retrolateral basal projection (Figs. 3, 7); subtegulum prolateral; tegulum covered by conductor; median apophysis hook shaped (Figs. 1, 7); embolus surrounding tegulum, supported by conductor; conductor sclerotized ventrally, with retrolateral laminar projection supporting embolus tip (Figs. 2, 8). Epigynum: formed by single plate, slightly sclerotized, with anterior hood (Fig. 5); spermathecae rounded; fertilization ducts short, emerging from spermathecal base (Fig. 6).

Composition.—Two species: *Toca bossanova* new species and *T. samba* new species

Distribution.—Southern and southeastern Brazil.

Toca bossanova new species

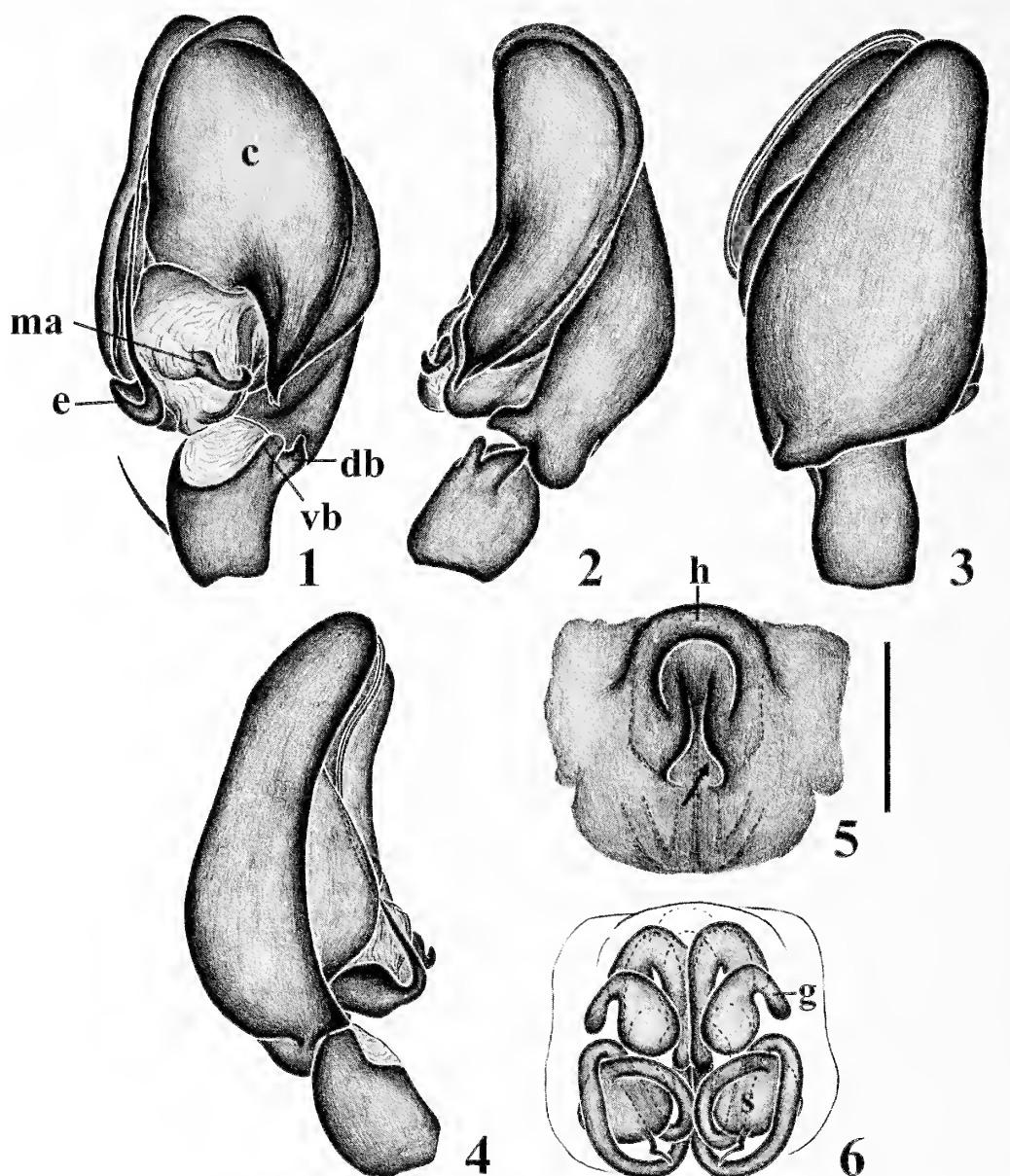
Figs. 1–6

Type material.—Male holotype from Fazenda Ranchinho Porto da Roça, Petrópolis, 22°30'39"S, 43°11'4"W, Rio de Janeiro, Brazil, 12–14 November 1999, deposited in IBSP 62920; female paratype from the same locality, 8–15 February 2000, Equipe Biota, deposited in IBSP 62919; male paratype from the same locality, 15–16 August 2001, Equipe Biota, deposited in IBSP 90669.

Etymology.—The species epithet is a Portuguese noun that refers to a popular rhythm of Brazilian music.

Diagnosis.—*Toca bossanova* can be distinguished from *T. samba* by the elongated cymbium and conductor, the elongated retrolateral projection of the conductor, and the slender and thin median apophysis on the male palp (Figs. 1–4). The females can be recognized by the presence of an anterior epigynal hood (Fig. 5)

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Figures 1-6.—*Toca bossanova*. 1-4 male palp: 1. Ventral view; 2. Retrolateral view; 3. Dorsal view; 4. Prolateral view. 5-6 Epigynum: 5. Ventral view (arrow points to left copulatory opening); 6. Dorsal view. Abbreviations: c, conductor; db, dorsal branch of retrolateral tibial apophysis; e, embolus; g, glandular projection; h, hood; lp, laminar projection of tegulum; ma, median apophysis; s, spermathecae; vb, ventral branch of retrolateral tibial apophysis.

and elongated copulatory ducts, overlaid with small glands (Fig. 6) in the epigynum.

Description.—*Male* (IBSP 62920). Total length 3.40. Carapace 1.50 long and 1.40 wide. Clypeus 0.07 high. Eye diameter: AME 0.10, ALE 0.08, PME 0.10, PLE 0.10. Leg measurements: I: femur 1.60/ patella 0.50/ tibia 1.80/ metatarsus 1.70/ tarsus 0.60/ total 6.20; II: 1.70/ 0.45/ 1.85/ 1.90/ 0.60/ 6.50; III: 1.80/ 0.40/ 1.75/ 1.85/ 0.70/ 6.50; IV: 1.90/ 0.40/ 1.60/ 2.10/ 0.90/ 6.90. Leg formula: 42=31. Leg spination: tibiae I and II with eight ventral pairs of spines; metatarsi I and II with six ventral pairs of spines. Abdomen brown with posterior area white. Palp: ventral branch of RTA laminar (Fig. 1); prolateral area of tegulum visible in ventral view, with laminar process (Fig. 4).

Female (IBSP 62919). Total length 4.40. Carapace 1.60 long and 1.60 wide. Clypeus 0.08 high. Eye diameter: AME 0.10, ALE 0.08, PME 0.12, PLE 0.12. Leg measurements: I: femur 1.50/ patella 0.50/ tibia 1.80/ metatarsus 1.60/ tarsus 0.50/ total 4.90; II: 1.80/ 0.60/ 1.80/ 1.60/ 0.60/ 6.40;

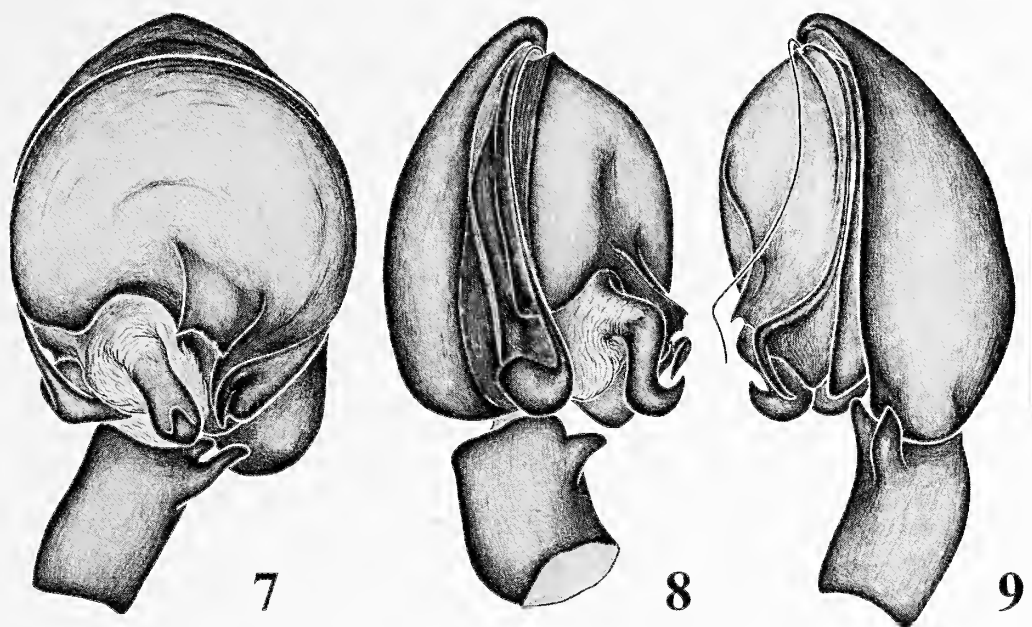
III: 1.80/ 0.50/ 1.60/ 1.80/ 0.70/ 6.40, IV: 1.80/ 0.50/ 1.50/ 1.80/ 0.70/ 6.30. Leg formula: 2=341. Leg spination: tibiae I and II with eight ventral pairs of spines; metatarsi I and II with six ventral pairs of spines. Coloration of the abdomen as in male. Epigynum as in generic description.

Additional material examined.—None.

Distribution.—State of Rio de Janeiro, Brazil.

Toca samba new species
Figs 7-9

Type material.—Male holotype from Morro do Cabral, Lagoa, Tijucas do Sul, 25°55'37"S, 49°10'44"W, Paraná, Brazil, November 2000, J. Ricetti, deposited in IBSP 39239; male paratype from Parque Estadual de Vila Velha, Ponta Grossa, 25°4'60"S, 50°8'60"W, Paraná, Brazil, 8 December 1986, Profaupar/CIIF, deposited in IBSP 62915; male paratype from Mata Grande, Parque Estadual do Ibitipoca, Lima Duarte, 21°51'10"S, 43°47'60"W, Minas Gerais, Brazil, 27-29 October 1997, B. M. Souza, deposited in IBSP 23812.



Figures 7–9.—*Toca samba*. Male palp: 7. Ventral view; 8. Prolateral view; 9. Retrolateral view.

Etymology.—The species epithet is a Portuguese noun which refers to a popular rhythm of Brazilian music.

Diagnosis.—*Toca samba* can be distinguished from *T. bossanova* by the rounded cymbium and conductor, median laminar projection on the conductor, and robust median apophysis on male palp (Figs 7–9).

Description.—*Male* (IBSP 39239): Total length 4.00. Carapace 1.60 long and 1.50 wide. Clypeus 0.08 high. Eye diameter: AME 0.10, ALE 0.08, PME 0.10, PLE 0.10. Leg measurements: I: femur 1.80/ patella 0.60/ tibia 2.00/ metatarsus 1.80/ tarsus 0.70/ total 6.90; II: 1.90/ 0.60/ 2.00/ 1.80/ 0.80/ 7.10; III: 2.10/ 0.50/ 1.90/ 1.90/ 0.90/ 7.30; IV: 2.20/ 0.50/ 2.00/ 2.20/ 1.00/ 7.90. Leg formula: 4321. Leg spination: tibiae I and II with eight ventral pairs of spines; metatarsi I and II with six ventral pairs of spines. Abdomen medially pale brown, with two anterior white spots, lateral area brown and posterior area white. Palp: ventral branch of RTA elongated (Fig. 9); subtegulum reduced, not visible in ventral view.

Female: Unknown.

Additional material examined.—None.

Distribution.—States of Paraná and Minas Gerais, Brazil.

DISCUSSION

To date, there are only two Caloeteninae genera described from South America: *Caloctenus* and *Gephyroctenus*. *Caloctenus* contains four valid species and can be distinguished by leg spination, carapace shape, strongly sclerotized male palpal tibia at apex, and median apophysis with an apical beak. These characters were considered apomorphic by Silva (2004). *Gephyroctenus* contains eight species and can be distinguished by the following synapomorphies: a cymbial retrolateral groove, retrolateral origin of embolus, long and thin embolus, median apophysis with a subdistal hook, hyaline projection close to the embolus base in the male palp, fused median and lateral fields in a single epigynal plate, copulatory opening located dorsally in an atrium, and elongated copulatory ducts surrounding the spermathecae in the female epigynum (Polotow & Brescovit 2008). The two species described in this paper cannot be assigned to these previously described genera. In addition to the unique morphological characters on the male palp and female epigynum, as described above, they lack the apomorphic features that characterize *Caloctenus* and *Gephyroctenus*.

Caloctenus and *Gephyroctenus* are closely related by the presence of four retrolateral teeth in the chelicerae, reduced anterior lateral eye

lenses, and cylindrical glands with an enlarged base on the posterior median spinnerets (Silva 2003). *Toca* also has reduced anterior lateral eye lenses, but five to six retrolateral teeth. The presence of the cylindrical glands with an enlarged base on the posterior median spinnerets in *Toca* should be confirmed in the future with scanning electronic microscopy.

The males of *Toca* share the long and filiform embolus on the male palp with *Gephyroctenus*. The females of *Toca* resemble the type species of *Diallomus*, *D. fulliginosus*, from Sri Lanka (female type specimen deposited in the MNHN, examined), both by the single, slightly sclerotized epigynal fold and the anterior hood on the female epigynum. Therefore, the relationship of *Toca* new genus to other Caloeteninae genera awaits cladistic analysis with all the genera assigned to Caloeteninae and representatives of the remaining subfamilies of Ctenidae.

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LITERATURE CITED

- Platnick, N.I. 2008. The World Spider Catalog, Version 8.5. American Museum of Natural History, New York. Online at <http://research.amnh.org/entomology/spiders/catalog/index.html>
- Polotow, D. & A.D. Brescovit. 2008. Revision of the Neotropical spider genus *Gephyroctenus* (Araneae: Ctenidae: Caloeteninae). *Revista Brasileira de Zoologia* 25:705–715.
- Silva, D. 2003. Higher-level relationships of the spider family Ctenidae (Araneae: Ctenoidea). *Bulletin of the American Museum of Natural History* 274:1–86.
- Silva, D. 2004. Revision of the spider genus *Caloctenus* Keyserling, 1877 (Araneae, Ctenidae). *Revista Peruana de Biología* 11:5–26.
- Simon, E. 1897. *Histoire naturelle des araignées*. Librairie encyclopédique de Roret, Paris 2:1–192.

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Huber, B.A. & W.G. Eberhard. 1997. Courtship, copulation, and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). *Canadian Journal of Zoology* 74:905–918.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66. In *Spider Communications: Mechanisms and Ecological Significance*. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Platnick, N.I. 2009. The World Spider Catalog, Version 9.5. American Museum of Natural History, New York. On-line at <http://research.amnh.org/entomology/spiders/catalog/INTRO1.html>

Roewer, C.F. 1954. *Katalog der Araneae, Volume 2a*. Institut Royal des Sciences Naturelles de Belgique, Bruxelles. 923 pp.

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